Arne R. Panesar

EVOLUTION IN WATER MITES (HYDRACHNELLAE, ACTINEDIDIA, ACARI)
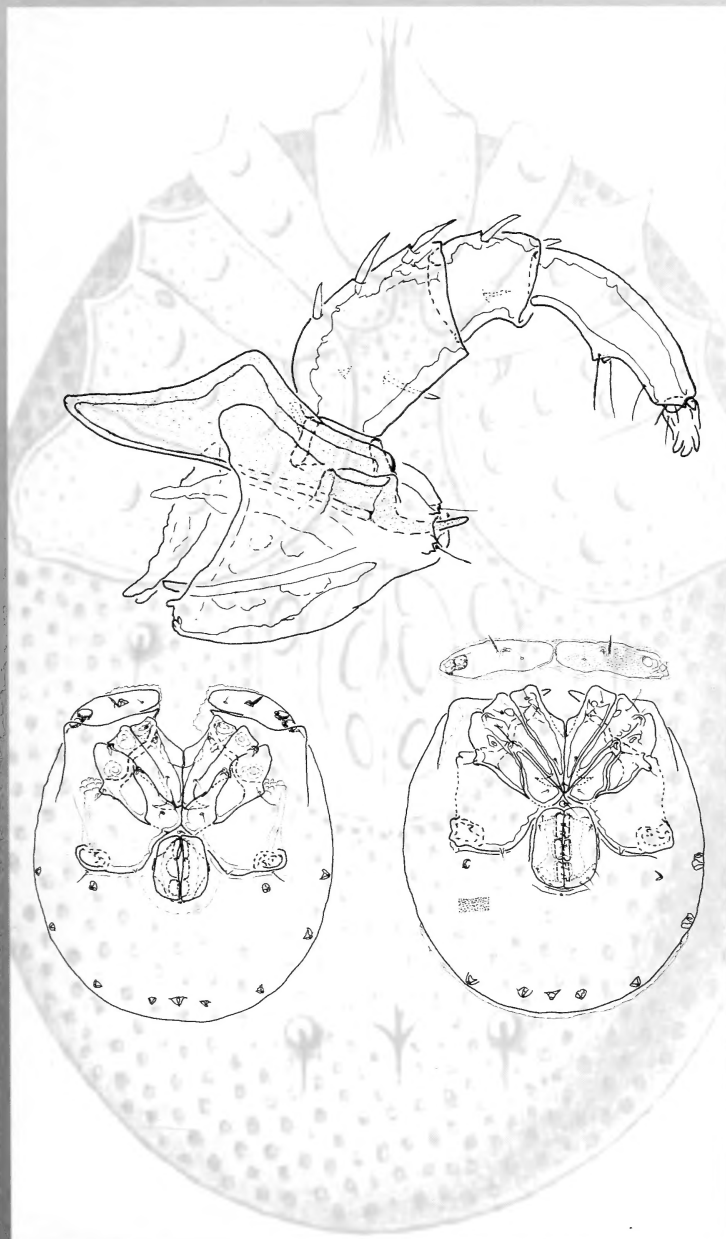
A revision of
the Anisitsiellidae
KOENIKE, 1910

BONNER ZOOLOGISCHE MONOGRAPHIEN

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CONTENTS

ABSTRACT

A cladogram for the Hydrachnellae (water mites) superfamilies resulting from a parsimony calculation is presented and discussed [(Hydryphantoidea (Hygrobatoidea (Wandesioidea (Hydrachnoidea (Hydrovolzioidea (Piersigioidea (Eylaoidea, Limnocharoidea) (Length = 13; Ci = 92; Ri = 87)]. The information for the data set was gained during the analysis of studies on body plans and segmental remnants in Hydrachnellae (Tuzovski 1987, Wiles 1997, Weigmann 2001).

The concept of the superfamily Hygrobatoidea Koch, 1824 (*sensu* Tuzovski 1987) is confirmed in the present study by the above-mentioned analysis. The families Anisitsiellidae and Limnesiidae, in traditional systems (e.g., Cook 1974) placed within two separate superfamilies, are both placed within the Hygrobatoidea in the system of Tuzovski (1987). This study proves that they are closely related to each other.

Several years of investigations on the water mite fauna of the Himalayas have yielded new genera and species belonging to the Anisitsiellidae-Limnesiidae Complex, one of them intermediate between the families Anisitsiellidae and Limnesiidae. To resolve taxonomic contradictions in current systematics, a critical revision of the 132 species and 31 genera placed under the family Anisitsiellidae Koenike, 1910, is undertaken. The revision leads to the proposal of major changes in the taxonomic system, including the suggestion of a new family and two new subfamilies.

The family Bandakiopsidae (fam. nov.) is proposed for 3 of the genera formerly placed under Anisitsiellidae (*Bandakiopsis, Cookacarus, Oregonacarus*). All the other Anisitsiellidae genera are included in one of the 3 following Limnesiidae subfamilies: Bandakiinae (subfam.nov.), Bharatoniinae (subfam. nov.) and Anisitsiellinae (stat. nov.). From the material collected in India, 2 new genera (*Shivatonia*, Bharatoniinae, Limnesiidae, and *Paddelia*, Anisitsiellinae, Limnesiidae) and 13 new species (*Bandakiopsis phaluti, Bandakia curvipalpis, Bandakia gangetica, Bandakia himachali, Bandakia kulluensis, Utaxatax brahmeri, Utaxatax crassipalpis, Utaxatax gereckei, Utaxatax parvati, Shivatonia acetabulensis, Paddelia eichhorniae, Nilotonia cooki*, and *Nilotonia shivai*) are described. New synonyms suggested include: Anisitsiellidae as junior synonym to Limnesiidae, Nilotoniinae as junior synonym to Anisitsiellinae, *Mamersellides* as junior synonym to *Anisitsiella*, *Tadagatonia* as junior synonym to *Nilotonia*, *Nilotonia schwoerbeli* as junior synonym to *Nilotonia emarginata*, *Nilotonia buettikeri* as junior synonym to *Nilotonia robusta*, and *Mamersella anomala* as junior synonym to *Limnesia auspexa*.

On the basis of comparative morphological studies, it is proposed to distinguish within the Hygrobatoidea (*sensu* Tuzovski) (1.) the "*Sperchon*-like", (2.) the "*Limnesia*-like", and (3.) the "*Hygrobates*-like and *Mideopsis*-like" families. The organizational form of the provisory genital field in the nymphal stage is used as one of the key characters to the family groups. The "basis ring-sclerites" of the genital acetabula in the adult stage and their tendency to fuse to each other and to the genital flaps is documented. The gradual fusion of the enlarged ring-sclerites to the genital flaps closely connects certain genera that were formerly placed under the Anisitsiellidae to genera of the Limnesiidae.

Key words: Water mites, Hydrachnellae, Actinedidia, Acari, evolution, revision, Limnesiidae, Bandakiopsidae (fam. nov.), Bandakiinae (subfam.nov.), Bharatoniinae (subfam. nov.), Anisitsiellinae (stat. nov.), *Shivatonia* (gen. nov.), *Paddelia* (gen. nov.), *Bandakiopsis phaluti* (sp. nov.), *Bandakia curvipalpis* (sp. nov.), *Bandakia gangetica* (sp. nov.), *Bandakia himachali* (sp. nov.), *Bandakia kulluensis* (sp. nov.), *Utaxatax brahmeri* (sp. nov.), *Utaxatax crassipalpis* (sp. nov.), *Utaxatax gereckei* (sp. nov.), *Utaxatax parvati* (sp. nov.), *Shivatonia acetabulensis* (sp. nov.), *Paddelia eichhorniae* (sp. nov.), *Nilotonia cooki* (sp. nov.), *Nilotonia shivai* (sp. nov.), Hydryphantoidea, Hygrobatoidea, Wandesioidea, Hydrachnoidea, Hydrovolzioidea, Piersigioidea, Eylaoidea, Limnocharoidea.

ACKNOWLEDGMENTS

ABBREVIATIONS

1-L-6	first leg, segment 6
Ae	lateral seta on anal segment "A" (s.T.)
Ai	medial seta on anal segment "A" (s.T.)
C1-C4	coxa 1-4, coxa (= epimera)
CAP	private collection of Panesar, Freiburg, Germany
Ce	lateral seta on segment "C" (s.T.)
Cg2	coxoglandulare 2 (= E2 in Wiles 1997)
Cg4	coxoglandulare 4 (= E4 in Wiles 1997)
Ci	medial seta on segment "C" (s.T.)
CNC	collection Smith *et al.*, Canadian National Collection, Biosys. Res. Inst., Ottawa
CNM	collection Cook *et al.*, in the Chicago Natural History Museum
CRG	private collection Gerecke, Tübingen, Germany
Dh1-Dh4	dorsohysterosomal seta 1-4
DS	dorsal shield
Ex1, Ex2	setal pairs on anal segment of larval stage
Feh	antennal seta on first segment (s.T.)
Fp	antennal seta on second segment (s.T.)
Gn	gnathosoma (= capitulum = camarostom)
He	lateral seta on segment "H" (s.T.)
Hi	medial seta on segment "H" (s.T.)
Le	lateral seta on segment "L" (s.T.)
Lh1-Lh4	laterohysterosomal seta 1-4
Li	medial seta on segment "L" (s.T.)
MONZ	Museum of New Zealand
NHB	collection Bader, Walter, Schwoerbel *et al.*, at Naturhistorisches Museum Basel, Schweiz
NMB	collection Panesar *et al.* at Naturhistorisches Museum Basel, Schweiz
NHP	collection Sokolow *et al.* at Museum of Natural History, Petersburg, Russia
Oe	lateral seta on segment "O" (s.T.)
Oi	medial seta on segment "O" (s.T.)
P1-P5	first, second ... segment of palp
Pe	lateral seta on preanal segment "P" (s.T.)
pGF	provisory genital field
Pi	medial seta on preanal segment "P" (s.T.)
ROM	collection of the Department of Invertebrate Zoology at the Royal Ontario Museum
s.T.	*sensu* Tuzovski 1987
sC1-sC5	setae on coxae of larval stage
Sce	lateral seta on segment "Sc" (s.T.)
Sci	medial seta on segment "Sc" (s.T.)
Se	lateral seta on segment "S" (s.T.)
Si	medial seta on segment "S" (s.T.)
SW-H	Swimming-hairs
SMF	collection K.O. Viets *et al.*, at Senckenberg Museum Frankfurt, Deutschland
SMH	collection Lundblad *et al.*, at Swedish Museum of Natural History, Stockholm, Sweden
Ve	lateral seta on segment "V" (s.T.)
Vh1-Vh4	ventrohysterosomal seta 1-4
Vi	medial seta on segment "V" (s.T.)
VS	ventral shield
ZSI	Zoological survey of India

1. INTRODUCTION

Regarding our knowledge on water mites (Hydrachnellae), the Himalayas are still a "terra incognita." Hydrachnellae from India (excluding the Himalayas) were known previously, mainly through the classical work of Cook (1967) in which 173 species were discussed.

During several visits to India (1989–1996), more than 7000 specimens of Hydrachnellae were collected for this study, most of them from the southern Himalayas. About 100 specimens thereof are examples of rarely found taxa of "anisitsiellid-like" mites, among them several new genera and species. The material seemed promising in helping to elucidate the problematic relationship between the families Anisitsiellidae and Limnesiidae.

During the 20th century, more than 3000 new species of Hydrachnellae from nearly all continents were described by Lundblad, Viets, Cook, Schwoerbel and others, leading to the roughly 6000 species currently known to science (Schwarz *et al.* 1998). Numerically, Hydrachnellae represent a highly successful lineage of the Actinedida (Actinotrichida, Acari).

The large number of recently described species was accompanied by increasing contradictions in systematics. Especially the family Anisitsiellidae was characterized by Cook (1974) as the "dumping place" for all taxa which do not fit into neighboring and better defined families. The clarification of the taxonomic and phylogenetic relationships of the Anisitsiellidae was therefore selected as the main objective of the present study.

Hydrachnellae are secondarily adapted to aquatic life and are found in almost all kinds of aquatic habitats. They may occur in high densities, with more than 200 specimens per square meter (B.P. Smith 1988). The group often forms a part of the zoocoenosis in perennial and temporary stagnant waters, in springs, in seepage areas, in hyporheic waters, in streams and in rivers.

With the help of a parasitic "aerial" larval stage, the otherwise strictly aquatic Hydrachnellae are able to effectively exploit the waterbodies of a region. The larvae are found attached to insects belonging to various groups such as Hemiptera, Coleoptera, Odonata, Trichoptera or Diptera, and with the flying stages of the insect hosts the Hydrachnellae change from one waterbody to another.

During the second half of the 20th century, an increasing number of investigations dealt with ecological and phylogenetic questions. The enormous variety in body shapes and exoskeletal structures of Hydrachnellae (Fig. 1) led several authors to the opinion that this group is a polyphyletic assemblage of taxa which independently have invaded the aquatic habitat (Smith & Cook 1991, Weygoldt 1996).
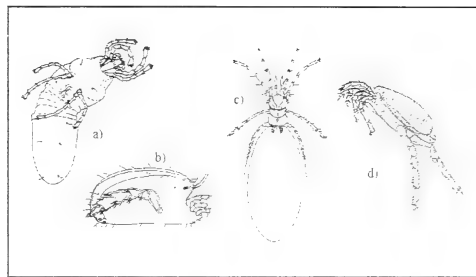
FIG. 1. Hydrachnellae exhibit an enormous variety of body shapes and exoskeletal structures: (a) *Euwandesia sensitiva*, (b) *Frontipodopsis reticulatifrons*, (c) *Psammolimnesia mexicana*, (d) *Feltria mira* [Figs. from Schwarz *et al.* (1998)].

However, a series of comparative studies on different character complexes suggests that Hydrachnellae are monophyletic. The autapomorphies stated for the Hydrachnellae include (1) the spermatophore being resistant to osmotic stress (Witte 1984, 1991), (2) the highly specialized male genital skeleton (Barr 1972), (3) the acetabula plate with a highly typical kind of porosity in nymphs and adults (Barr 1982), and (4) the common ground plan of chaetotaxy in all taxa and life stages (Tuzovski 1987, Welbourn 1991, Wiles 1997).

Hydrachnellae, systematic position and origin

Several characters connect the Hydrachnellae with the other Parasitengona. The larvae are heteromorphic in all Parasitengona (including Hydrachnellae), but they are homeomorphic in the other Actinedida. In the Parasitengona (including Hydrachnellae), the protonymphs and tritonymphs are inactive and only partially expressed stages which develop in the cuticle of the preceding stages, while in the other Actinedida they are active and free-living stages.

Early derivate Hydrachnellae share the two-segmented larval femur subdivided into basifemur and

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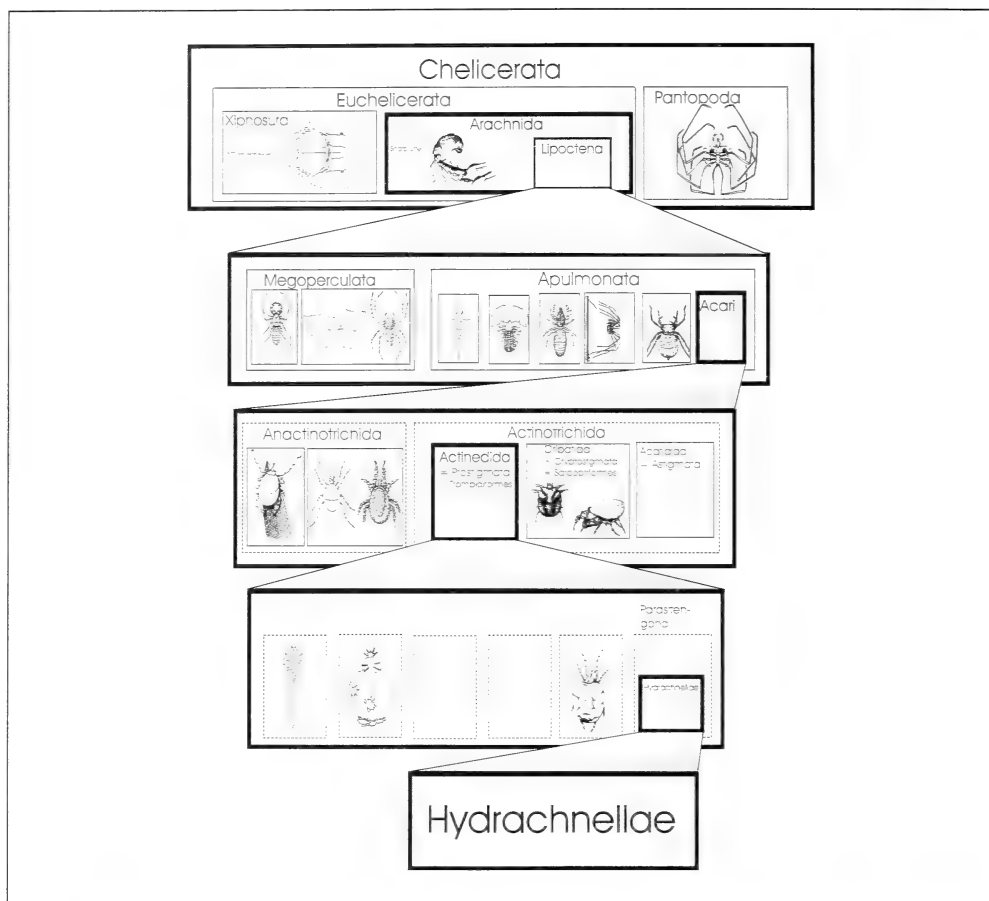
FIG. 2. Systematic position of Hydrachnellae in the Chelicerata. Systematics of Chelicerata following Weygoldt (1996). Systematics of Actinedida following Kethley (1990). Systematic position of Hydrachnellae following Tuzovksi (1987).

telofemur with some of the terrestrial Parasitengona (Kethley 1990). Apart from the Hydrachnellae, some other subgroups of the Acari (e.g., Halacaridae, Stygo-thrombidiidae, some Oribatidae) have convergently invaded the aquatic habitat. The term water mites may refer to all these groups or only to some of them (e.g., Halacaridae and Hydrachnellae). In the present study the term "water mites" refers to the Hydrachnellae (*sensu* Tuzovski 1987, s.T. in text) exclusively.

It is presumed that Hydrachnellae evolved from an ancestral terrestrial Parasitengona (Mitchell 1957, Davids & Belier 1979). The parasitengone ancestor may have resembled certain soft-bodied extant Hy-

dryphantoidea (Wiggins *et al.* 1980, Smith & Oliver 1986). Distributional data and host associations indicate that the Hydrachnellae originated no later than during the Triassic or Jurassic period (Smith & Cook 1991, 1999).

Hydrachnellae are treated in this study as a separate monophyletic phalanx of the cohort Parasiten-gona. The Parasitengona are one of the six cohorts in the suborder Actinedida (= Prostigmata = Trombidi-formes) which belong to the Acari (Tuzovski 1987).

The autapomorphic character states for the Hy-drachnellae themselves, and synapomorphic character states, shared between Hydrachnellae and higher taxa such as Chelicerata or Acari, are given in Table 1.

Evolution of the water mite exoskeleton

Today the evolution of the adult exoskeleton among water mites is commonly understood as an adaptation of the water mite body to apotypical behavior (Mitchell 1957, Smith & Cook 1991, 1999). For example, plesiotypically water mite larvae run on the water surface to locate their hosts, while apotypically they are able to swim and hunt their hosts underwater. As water is a medium with a higher density than air, stronger muscles are needed when larval legs have to move fast and continuously to permit rapid swimming. Larger and more stable attachment sites for the enlarged muscles are provided in the body wall in the form of enlarged or fused coxae as well as by enlarged or fused plates. These structures form the partial or complete water mite exoskeleton (Mitchell 1957).

Various forms of apotypic behavior are mentioned as reasons for the enlargement of muscles and attachment sites in adults, such as (1) swimming, (2) walking against a water current, (3) carrying a drop of

TABLE 1. Apomorphic character states of taxa leading to the Hydrachnellae (data as stated, otherwise from Kethley 1990, Schmitt 1996, Weygoldt 1996). [ ] = Characters given in brackets are apomorphic for higher taxa but are secondarily reduced in lower taxa.

Taxon	Apomorphic character states
Euarthropoda	- articulated legs, [complex eyes], cuticula with α-chitin
Chelicerata	- reduction of first antennae
	- first mouthparts developed into chelicerae
	- [body divided into prosoma and opistosoma]
	- five pairs of legs, with usually the first pair transformed into pedipalps
Arachnida	- slit organs for mechano- or vibrato-reception
	- extra-intestinal digestion
Acari	- characteristic acarine body plan with gnathosoma and idiosoma
	- larva hexapod (possibly a synapomorphy with Ricinulei)
	- 3 nymphal stages (possibly a synapomorphy with Ricinulei)
	- spermatophores with stalk and foot
	- excretory pore plate slit-like
Actinotrichida	- setae with protein actinopilin
Actinedida	- trachea, if present, reduced to region of gnathosoma
	- colon ending blind
	- excretory organ ending in excretory pore homolog of anus
Parasitengona	- larva heteromorphic (all life stages homeomorphic in other Actinedida)
	- proto- and tritonymph reduced to immobile stages, which develop in the cuticle of the preceding stage
	- prelarva not known to feed, often immobile with legs reduced
Hydrachnellae	- prelarva reduced to a stage developing in the cuticle of the egg
	- reduction of supracoxal seta "e", companion seta associated with phi and omega on leg I and companion seta associated with the dorsal eupathidium on tarsus I in larva (Welbourn 1991)
	- palpal genu of the larva with two setae (only one is present in terrestrial Parasitengona) (Welbourn 1991)
	- unique morphology of male genital skeleton (Barr 1972)
	- specialized perforated surface of the acetabula (osmoregulatory organs) in nymphs and adults (Barr 1982)
	- common ground plan of the idiosomal chaetotaxy in all life stages (Tuzovski 1987)
	- spermatophores adapted to osmotic stress (Witte 1984, 1991)
	- adults purely aquatic and spermatophores transferred under water

water on a semi-dry surface and (4) burrowing in the sediment. The hypothetical ancestor of the Hydrachnellae was most probably a mite walking slowly below stagnant water on the substratum. For this ancestor, all the behavioral adaptations go together with the invasion of new habitats: the invasion of the water column (swimming), of running waters (walking against a water current), of the thin water film at the water's edge in seepage areas (carrying a drop of water) and of the hyporheic interstitial habitat (burrowing in the substratum) (Smith & Cook 1991). Hygrobatoidea (s.T.) are found in all these habitats and the development (or secondary reduction) of exoskeletal parts in this group took place convergently several times.

According to Smith & Cook (1991, 1999), by late Pangean times evolution within water mites had produced basic communities of essentially soft-bodied species living in temporary and permanent standing water, and partly to fully sclerotized species living in emergent groundwater, lotic, and interstitial habitats. The subsequent phylogeny of Hydryphantoidea and Hygrobatoidea (s.T.) during late Mesozoic, Tertiary, and Quaternary times appears to have followed a recurring pattern of extended periods of gradual evolution leading to specialization within particular habitats, punctuated by episodes of relatively rapid and dramatic invasion of new habitats.

Considering the extension of sclerotization as a phylogenetically significant character was one of the major mistakes in the phylogenetic interpretation of the morphological characters of anisitsiellid-like water mites. It has already been pointed out by Cook (1974) that due to the presence of intermediate taxa, the two subfamilies Anisitsiellinae and Nilotoniinae now grade completely into each other in the extent of sclerotization. However, for practical reasons and in absence of a better theory, Cook treats the subfamilies as valid. Until today the two Anisitsiellidae subfamilies (Anisitsiellinae and Nilotoniinae) have been characterized as highly sclerotized versus soft-bodied species (Smith & Cook 1991). Bader (1980) refers to the extent of sclerotization when he suggests raising the two subfamilies to family level.

Among anisitsiellid-like water mites, soft-bodied forms are found as well as fully sclerotized species with complete dorsal and ventral shields in several genera. As an example, a transformation series from smaller platelets into complete ventral and dorsal shields in the genus *Nilotonia* (Anisitsiellinae, Limnesiidae) is shown (Fig. 3).
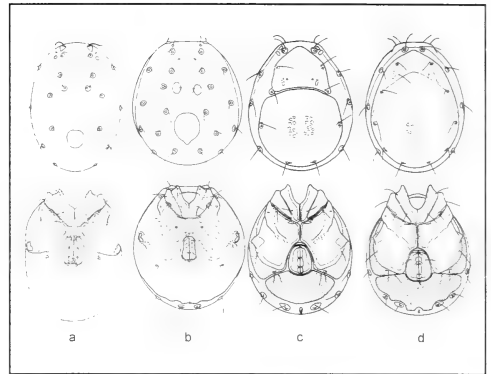
FIG. 3. Stabilisation of the idiosoma wall in *Nilotonia* (Anisitsiellinae, Limnesiidae): (a) *Nilotonia navina*, (b) *Nilotonia cooki* sp. nov. (cf. below), (c) *Nilotonia scutata*, (d) *Nilotonia testudinata* [Figs. a, c, d from Cook 1966; Fig. b from Cook 1967].

Mitchell (1958) gave an explanation of, why shape and size of exoskeletal sclerites are not necessarily useful for higher systematics in Hydrachnellae. He indicated that the evolution of a somatic exoskeleton took place comparatively late in the evolution of the Hydrachnellae, especially if compared with the early development of somatic chitinization of the segments in Insecta. Therefore, differing from the stable set of sclerites found among insects, we find spontaneous secondary sclerotization of the idiosomal integument in nymphs and adults of water mites leading to many different combinations of plates and platelets.

In the Anisitsiellidae-Limnesiidae complex, the extent of sclerotization or the combination of plates may be useful for lower taxonomy but they are misleading for higher systematics and phylogenetic approaches in almost all cases.

Life history and behavior

Research on life history and behavioral patterns contributes significant data to the interpretation of water mite evolution. Therefore a rough outline of the relevant results in this field is given below.

Typically there are three active and four quiescent stages in the life cycle of a water mite. Table 2 gives an overview of the different life stages and of the typical duration of these stages in Hygrobatoidea (s.T.):

Eggs and prelarva. Eggs are always laid under water. Number of eggs per clutch range from one to more

TABLE 2. Life stages in water mites differ considerably in duration between the different superfamilies; in this table average durations of life stages for members of the superfamily Hygrobatoidea are given (s.T. = *sensu* Tuzovski 1987). [Data from Smith & Oliver (1986) (review), Meyer (1985), Gerecke *et al.* (1999), and Gerecke (pers. comm.)].

Life stage	Quiescent: Q Active: A	Typical life time per stage in Hygrobatoidea (s.T.)	Comments
1. Egg	Q	1-6 weeks	
2. Prelarva	Q	a few days	remains in the egg cuticula
3. Larva	A		
A. hatching period		minutes to hours	
B. hunting period		up to a few weeks	
C. phoretic on preadult instar		up to a few weeks	
D. phoretic & parasitic on adult insect		a few hours up to a few days	
4. Protonymph	Q	days (little known)	remains in larval cuticula
5. Deutonymph	A	several months	
6. Tritonymph	Q	days-weeks (little known)	remains in deutonymphal cuticula
7. Adult	A	1-3 years	

than 2500 (Sokolow 1977). They are either covered with one sheet per egg or with a common sheet for the whole group of eggs.

In Hygrobatoidea (s.T.), egg clutches with a common sheet are found in *Sperchon, Lebertia*, Hygrobatidae, *Wettina*, and *Ljania* (clutch size 1–40). However egg clutches without a common sheet are found in the genus *Arrenurus*. The quiescent prelarva forms a cuticula inside the egg. The first molt of the prelarval stage leads to the active larva.

Larva. Generally the active larva hatches after a few weeks under water from the cuticula of the prelarva and the egg. With a few exceptions the larvae need an insect host to complete their life cycle.

Larval stages of different superfamilies vary: (1) in their host-finding behavior, (2) in the host range, (3) in the places preferred for engorgement, (4) in the amount of liquids taken up during the parasitic phase, (5) in the duration of the parasitic and phoretic life phase (reviews for 1–5 by Smith & Oliver 1976, 1986), and (6) in their impact on the host population (B.P. Smith 1988).

Larvae of extant Hydryphantoidea have a broader host range than all other evolutionary lineages. Their host range includes different orders of insects, and in some species even Hymenoptera and Collembola.

Other early derivate lineages use typically Hemiptera, Coleoptera or Odonata as hosts, while in Hygrobatoidea (s.T.) a high number of species is specialized on nematocerous Diptera (mainly Chironomidae). Other hosts of Hygrobatoidea include Diptera (Brachycera), Trichoptera (attacked by species of 6 genera), Odonata (attacked by some species of *Arrenurus* only) and Coleoptera larva (attacked by *Arrenurus globator* only).

While early derived Hydrachnellae possess larvae which hunt their hosts in an "aerial" environment – running around on the water surface or on adjacent vegetation – it is a convergently developed apotypical behavior of the Hygrobatoidea (s.T.), Hydrachnoidea and Acherontacaridae larva to locate their insect host under water. Hygrobatoidea (s.T.) are the only superfamily with species in which the larvae locate their host in the final preadult instar and then wait with engorgement until the terrestrial or "aerial" adult emerges.

The host has two basic functions for the larva: feeding it (parasitism) and transporting it to other waterbodies (phoresy). Apart from this, in some early derivate clades, the host helps the water mite species to survive the dry phase of temporary waterbodies. Larvae of species that are adapted to temporary pools engorge after a period of arrested development and

TABLE 3. Overview on the various hosts of the different superfamilies and on the different habitats of the hunting larva. [Data from Smith & Oliver (1986) (review), Gerecke *et al.* (1999), and Gerecke (pers. comm.)].

Superfamily	Habitat of the hunting larva	Habitat of the host while being located	Host range
Limnocharoidea	pleustic	pleustic / neustic	Hempitera, Odonata, Coleoptera
Eylaoidea	pleustic	neustic	Hempitera, Coleoptera
Piersigioidea	pleustic	neustic	Coleoptera (Hydrophilidae, Dytiscidae)
Hydrovolzioidea			
- Hydrovolziidae	pleustic	pleustic / neustic	Hempitera, Diptera, Coleoptera
- Acherontacaridae	benthic	benthic	Coleoptera
Hydrachnoidea	neustic	neustic	Hemiptera, Coleoptera
Wandesioidea	pleustic	benthic (locating nymphal instar, attacking emerging adult)	Plecoptera
Hydryphyantoidea	pleustic	attacking pleustic, neustic and emerging hosts	various groups of Insecta, rarely Collembola or Hymenoptera
Hygrobatoidea	benthic / neustic	benthic / neustic (locating final preadult instar, attacking emerging adult; exception: *A. globator*)	most taxa: Diptera, some taxa: Trichoptera; *Arrenurus*: on Odonata, Diptera and one species on Coleoptera larvae
Pontarachnoidea	? (marine)	?	?

remain on hosts throughout the dry phase of the habitat, which may last as long as ten months in these cases (Cook 1974, Wiggins *et al.* 1980).

Feeding and growth during parasitism on long-lived hosts plays a major role in the larval phase of all early derivate lineages, with the exception of several Hydryphantoidea. In these cases, the larvae increase several hundred-fold in size and the parasitic phase during which they are engorged on the host may last two weeks or more. In contrast to this group of taxa in Hygrobatoidea (s.T.) and several Hydryphantoidea, phoretic dispersal seems to be the dominant function. Larvae increase only slightly in size and are often associated with short-lived insects, especially nematocerous Diptera. Larvae which are parasitic on nematocerous Diptera typically engorge rapidly and mature within a few hours. In these taxa the larval stage is specialized for phoretic dispersal. Therefore, in these cases feeding and growth take place during deutonymph and adult stage.

Protonymph. The protonymph (or nymphochrysalis) molts in the cuticula of the larva without hatching. It undergoes a pupal phase, the "first postlarval quiescence" (Böttger 1977). In Eylaoidea, the protonymph

develops while the larvae remains attached to the host and the deutonymph only leaves the host after the dry phase of the temporary waterbody. In most other clades the larva detaches from the host, tries to enter a waterbody, and the protonymph develops within the larval cuticula. In *Hydrodroma despiciens*, fully formed deutonymphs emerge from the larval and protonymphal cuticula and become active after a few days (Meyer 1985).

Deutonymph. The deutonymph is active, predaceous and similar to the adult in appearance, but equipped with a provisory genital field only (a plate in the area of the future genital field, but without an open gonopore). In the superfamilies Hydrachnoidea, Limnocharoidea, Eylaoidea, and most Piersigioidea, the parasitic larvae is the main growing stage and the duration of the deutonymphal stage is short, varying from only a few days to a few weeks. Especially in Hygrobatoidea (s.T.) the deutonymph is the main growing stage and may last several months. As a result, the deutonymphs in Hygrobatoidea (s.T.) are only partly sclerotized in order to allow growth of the body.

Tritonymph. The tritonymph (or imagochrysalis or "second postlarval quiescence") molts in the cuticula

of the deutonymph without hatching from it. It undergoes a pupal phase, which in *Hydrodroma despiciens* lasts a few days or weeks (depending on the temperature) (Meyer 1985).

Adult. The imago or adult water mite hatches from the skin of the deutonymph and matures sexually shortly after emergence. In certain Limnocharinae (Böttger 1977), adults undergo supernumerary molts. Imamura's (1952) statement about such additional molts also taking place in the strongly sclerotized Arrenuridae, has never found confirmation and is probably based on a misinterpreted observation.

Sperm transfer and pairing behavior

Water mite adults exhibit all modes of sperm transfer, from complete dissociation of the sexes to intromission (Proctor 1992a-c, 1997, 1998). The spermatophores are found and taken up by the female:
– with or without the help of signaling threads (which are glued to the substratum by males),
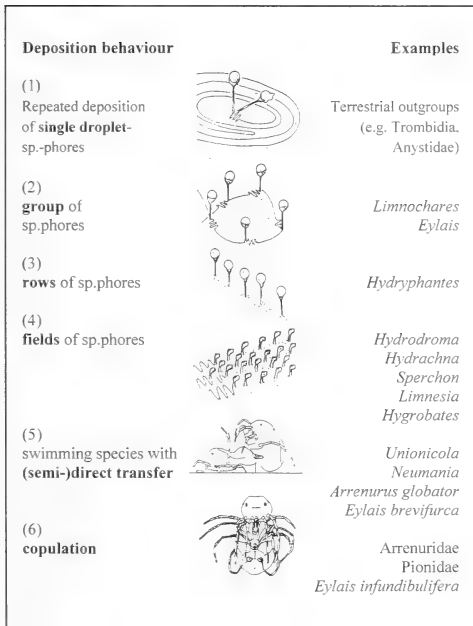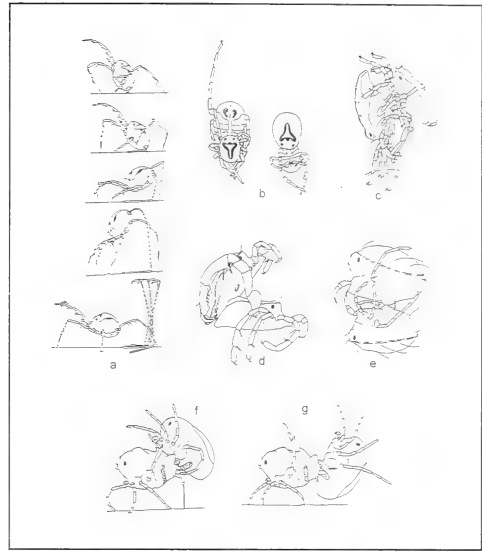
FIG. 5. Mating behaviour in Hydrachnellae: (a) *Unionicola* sp., (b) *Piona* sp. near *debilis*, (c) *Brachypoda versicolor*, (d) *Aturus scaber*, (e) *Midea orbicularia*, (f) and (g) *Arrenurus cuspidifer* [from Proctor (1992a)].

– with or without direct partner contact and/or mating behavior, and
– with or without copulation.

The pheromones of the females induce in some species the deposition of spermatophores, while in other species pheromones increase the number of spermatophores deposited.

In some species, the pheromones help females and males to locate the fields of spermatophores. In these cases the pheromones are emitted by the spermatophores. The fields of spermatophores are more attractive if large numbers of spermatophores are put together so that their pheromones can act as a "long-distance" signal.

Some females as well as some males were observed swimming rapidly past a field of spermatophores, at a distance of a few inches, and then changing their direction suddenly at a right angle in order to reach the field (Meyer 1985).

The males of some species produce large fields of several hundreds of spermatopohores and try to add their spermatophores to existing stands. In a few species, males destroy the spermatophores of other males or put their own spermatophores on top of existing ones.

Deposition behaviour	Examples
(1) Repeated deposition of **single droplet**-sp.-phores	Terrestrial outgroups (e.g. Trombidia. Anystidae)
(2) **group** of sp.phores	*Limnochares Eylais*
(3) **rows** of sp.phores	*Hydryphantes*
(4) **fields** of sp.phores	*Hydrodroma Hydrachna Sperchon Limnesia Hygrobates*
(5) swimming species with **(semi-)direct transfer**	*Unionicola Neumania Arrenurus globator Eylais brevifurca*
(6) **copulation**	Arrenuridae Pionidae *Eylais infundibulifera*

FIG. 4. A sequence of change in mechanisms of spermatophore (sp. phore) deposition, and of sperm transfer. The position suggested for *Limnesia* in this transformation series is between *Sperchon* and *Hygrobates* [based on Witte & Döring (1999), Fig. 9, p. 35].

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FIG. 6. Phylogeny based on evolutionary transformation of sperm transfer as suggested in Witte & Döring (1999). Phylogeny mainly based on Witte (1991), Witte & Olomski (in prep.) and Proctor 1992a, 1992b). Convergent evolution is shown for Eylaidae and late-derivative taxa of swimming mites. Limnesiidae are placed next to Hygrobates and Sperchontidae-Lebertiidae. Anisitsiellidae are not discussed, as there are no data available [Fig. from Witte & Döring (1999)].

Phylogenetic concepts referring to behavior

In his classic work, Mitchell (1957) points out the obvious connections between behavior of larvae and adults: the invasion of new habitats, modifications of morphology, and phylogenetically significant separation of clades. The reviews of Smith & Oliver (1976, 1986) show that larvae of different superfamilies are adapted to different taxa as hosts.

The investigations on the pairing behavior undertaken by Proctor (1992b) include a cladistic test referring to the sensory exploitation and the evolution of male behavior in water mites. Witte (1984, 1991) combined data on the morphology of the spermatophores with data on the pairing behavior. According to Witte & Döring (1999), original pairing behavior in the Parasitengona is probably a circling dance with the partners making tapping contacts. In Hydrachnellae such behavior seems to be (1) retained in a few species only (e.g., *Eylais extendens*), (2) re-duced to simple tapping contacts in several species (e.g., *Hydryphantes ruber, Hydrachna cruenta, Limnesia maculata*) and (3) lost where males deposit spermatophores without partner contact.

There are few data on spermatophores or pairing behavior available referring to species of the Anisitsiellidae-Limnesiidae complex. The few examples all refer to species of the genus *Limnesia*. With reference to the information on these species, Limnesiidae are placed next to Hygrobatidae in the system of Witte & Döring (1999), and both are placed next to Lebertiidae and Sperchontidae in a group that is characterized by males that deposit stalked spermatophores and signaling threads in smaller or larger fields (see Fig. 6).

The signaling threads are a "short-distance" guiding device, the initial function of which is probably to indicate the direction from which the female should approach the spermatophore in order to pick up the sperm (Witte 1991).
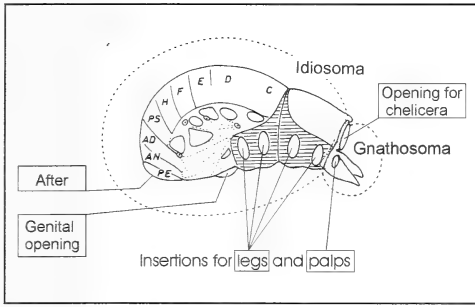
FIG. 7. Typical acarine body plan, with gnathosoma and idiosoma. Letters from "C" to "PE" are names for segments [modified from Moritz *et al.* (1994)].

Tapping contacts, as they have been reported, e.g., for *Limnesia maculata*, could serve as a preadaption to semi-direct and direct sperm transfer as well as to copulation – a behavior developed convergently several times in the more recently derived Hygrobatoidea (s.T.).

In many Hygrobatoidea (s.T.), the body form, or the form of a leg or leg segments, is altered in order to allow the sexual partner to attach, transport or store the spermatophores produced by the males.

The sexual dimorphisms in these characters or in the structures of the genital region (valves, acetabula) are common not only among Hygrobatoidea (*sensu* Tuzovski 1987) but also in most other superfamilies.

Harveys (1998) comment on earlier clado-gramms published by Witte (1984, 1991) is valid as well for the one of 1999 presented below (Fig. 6). Harvey points out that the cladograms published by Witte (1984, 1991) are not accompanied by a character matrix and are therefore difficult to assess. Analysis of this phylogeny is further hampered by the limited number of terminal clades (about 40 species out of 20 genera are included, presumably as exemplars of higher taxa). However the large number of characters utilised, particularly of spermatophore morphology and mating behaviour, shed considerable light on the evolution of these character systems within the context of the Parasitengona.

General morphology

Hydrachnellae exhibit the characteristic acarine body plan (Fig. 7) with a body divided into gnathosoma and idiosoma. The anterior region or gnathosoma bears the chelicerae and the palpus. The posterior region or idiosoma (body proper) externally bears the legs, reproductive structures and the anus.

The podosomal and opisthosomal separation, typically for ancestors of the Acari, is obliterated because the opisthosoma is fused to the segments of the podosoma that support legs III and IV, forming a new tagma, the hysterosoma (Fig. 8). The remaining elements of the original podosoma (the segments supporting legs I and II) comprise the propodosoma. The ventral part of the segments supporting the third and fourth pair of legs is named metapodosoma. The gnathosoma is formed by the ventral parts of anterior segments of the body. The combination of gnathosoma and propodosoma is called proterosoma.

True metameric segmentation is absent in Hydrachnellae due to the fusion of segments. However, the remnants of the ancestral segmentation are reflected in the presence of transverse rows of setae, associated glands, and slit organs (proprioreceptores), which form a series of segmental remnants (Kethley 1990). The nomenclatures used for these metameric structures in publications on Hydrachnellae differ from each other and from those used by other acarologists (see Chapter 4) to some extent.

Morphology of larval Hydrachnellae

The morphological structures of water mite larva are illustrated in the following two figures.
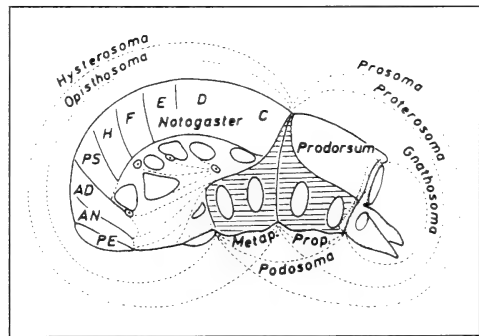
FIG. 8. Body regions of an actinedid mite. The prosoma is divided into propodosoma and metapodosoma. The gnathosoma is formed by the ventral parts of anterior body segments. The hysterosoma consists of the fused metapodosoma and opisthosoma. Dorsal sclerites of the proterosoma and opisthosoma are called prodorsum and notogaster respectively [modified from Moritz *et al.* (1994)].
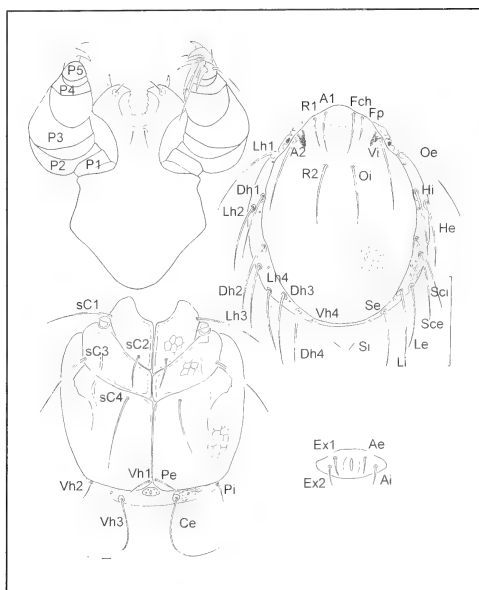
FIG. 9. Morphology of water mite larva (*Rutripalpus* sp.). Top left: gnathosomal base, palpi. Top right: DS. Bottom left: VS. Bottom right: anal plate. Abbreviations on the left half of VS, DS and anal plate as suggested in this work (see Chapter 4), those on the right half follow Tuzovski (1987) (for discussion of abbreviations for segmental remnants see Chapter 4). Scale = 100 μm (with reference to VS and DS only) [Figs. modified from Gerecke *et al.* (2000)].

Gnathosoma. A short gnathosoma bears stocky pedipalps, which have five free segments (P1–P5: trochanter, femur, genu, tibia, tarsus) that flex ventrally. In some ancient groups P5 is relatively long and cylindrical (Hydryphantidae, Thyadinae), but it is typically reduced to a dome or button-shaped pad in most Hygrobatoidea (s.T.).

A highly modified thick, curved seta is present dorsally at the end of P4. This seta is the homolog of the tibial "claw", which characterizes the pedipalp of most terrestrial Parasitengona and some related groups. The seta is secondarily reduced in several groups.

The paired chelicerae, each consisting of a cylindrical basal segment and a movable terminal claw, lie between the pedipalps. Among the Hygrobatoidea (s.T.), the basal segments are plesiotypically separate (e.g., Sperchontidae, Teutoniidae, Limnesiidae), but they are fused in nearly all derivate groups.
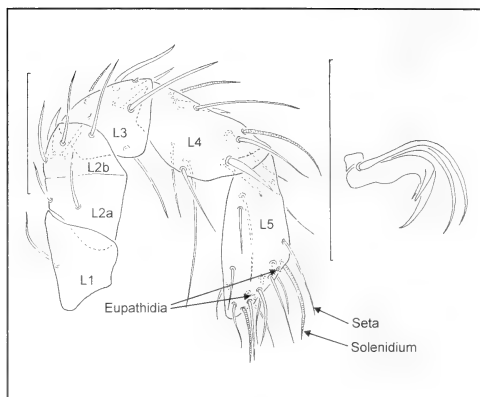
FIG. 10. Morphology of water mite larva: chaeto- and solenidiotaxy of legs. Left: first leg. Right: claw (for abbreviations see text) [Figs. from Gerecke *et al.* (2000). Drawings refer to a larva of *Rutripalpus* sp.] scale bars = 100 μm.

Idiosoma. Plesiotypically the idiosoma is mainly unsclerotized, as in extant Hydryphantoidea. The anterodorsal integument bears a pair of lateral eyes each with two lenses and plesiotypically a median eye-spot and a propeltidium. The metameric structures in the idiosoma wall include plesiotypically (Fig. 9) three pairs of coxae, four pairs of propodosomal setae (A1, A2, R1, R2), four pairs of hysterosomal setae dorsally (Dh1–Dh4), four pairs of hysterosomal setae laterally (Lh1–Lh4), four pairs of hysterosomal setae ventrally (Vh1–Vh4), two pairs of anal setae (Exp1, Exp2), a pair of setae called "Ce" and five pairs of slit organs.
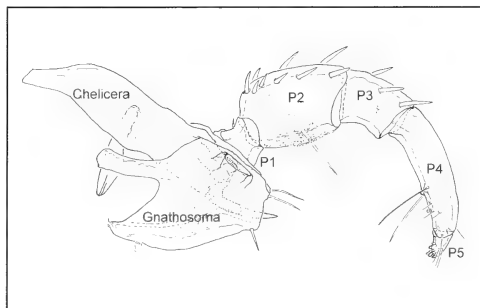
FIG. 11. Morphology of nymphal and adult Hydrachnellae: Lateral view of gnathosoma, with chelicera and medial view of left palpus [Fig. from *Nilotonia emarginata,* slide `96/191].
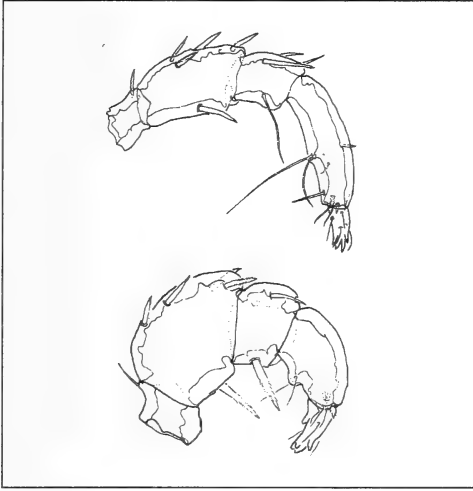
FIG. 12. The "anisitsiellid-like" palpus (top) and the "mamersopsid-like" palpus (bottom) are the two types of palpal shape found generally in the Anisitsiellidae-Limnesiidae complex. Palps of two species of *Utaxatax* (compare text and Chapter 6: "*Utaxatax*").

Morphology of Hydrachnellae deutonymphs and adults

In Hydrachnellae, deutonymphs and adults are quite similar and are therefore discussed together here. Differences are usually restricted to the extent of sclerotization and some characters in the genital region.

Gnathosoma. The gnathosoma is plesiotypically a simple, short channel, derived from extensions of the pedipalp coxae containing the esophagus (Mitchell 1962). A prolongation of the integument in form of a protrusible tube, connecting the gnathosoma to the idiosoma, has developed independently in several distantly related groups (e.g., Rhyncholimnocharidae, Clathrosperchoninae and certain Krendowskiidae). The paired pedipalps (= palpi = palps), inserted on

In Hygrobatoidea (s.T.) the median eye-spot and propeltidium are reduced. Seta "Ce" is found only in Limnocharoidea and Pontarachnoidea (cf. Chapter 4). Up to five setae belonging to the coxal plates are found (sC1-sC5). However, some of them are reduced in different clades (e.g., sC3 is reduced in most Limnesiidae).

Legs. The legs are inserted laterally on the coxal plates; in the plesiotypical condition they have six movable segments (trochanter, basifemur, telofemur, genu, tibia and tarsus). Plesiotypically the tarsus has a narrowed distal end but apotypically (as in Hydrachnoidea and Hygrobatoidea (s.T.) only), it is not narrowed but equipped with a distal excavation (Tuzovski 1987). In the superfamilies Hydrovolzioidea, Hydrachnoidea and Hygrobatoidea (s.T.), basifemur and telofemur are fused, resulting in a five-segmented leg (L1–L5).

The leg segments articulate to permit ventral flexion. The segments have characteristic complements of setae and solenidia (Fig. 10). The tarsi bear paired claws and claw-like empodia terminally. The interpretation of structures such as solenidia and eupathidia is disputed between Tuzovski (1987) and Prasad & Cook (1972) or Smith & Cook (1991).

FIG. 13. Morphology of adult Hydrachnellae: Idiosoma of *Nilotonia emarginata*. Top: ventral view. Bottom: dorsal view. For abbreviations see text and Chapter 4 [Fig. from slide IND 222/1996 CAP].
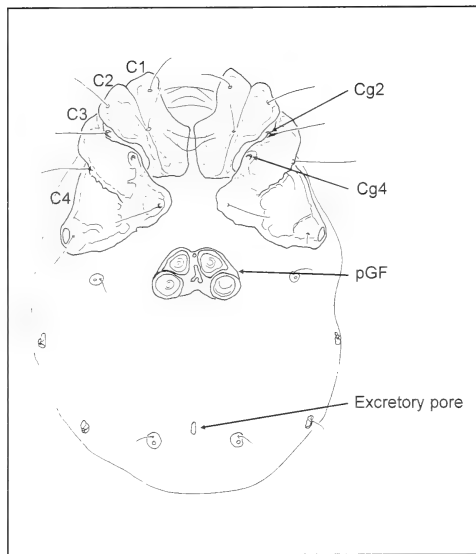
FIG. 14. Morphology of nymph: ventral view of idiosoma *Nilotonia emarginata* (Fig. from slide IND `96/191 ny). Nymphs differ from adults mainly in the provisory genital field (pGF). It is, in the nymphal stage, equipped with a lesser number of acetabula and no gonopore is found (for abbreviations see text).

the gnathosoma, have both tactile and raptorial functions. In the plesiomorphic condition, the palps have five movable segments (P1-P5), namely trochanter, femur, genu, tibia and tarsus, which are essentially cylindrical and articulate to allow ventral flexion. The tibia (P4) bears a thick, blade-like, dorsal seta distally in many ancient groups (e.g., Hydryphantinae, Tartarothyadinae, Pseudohydryphantinae). As in the larva, this seta is the homolog of the tibial "claw" of terrestrial relatives and it often makes the palps appear chelate. In derivate groups, other setae, along with various denticles and tubercles, may be elaborated to enhance the raptorial function of the palps. Segmentation of the palps is reduced by fusion in a few groups. The so-called "uncate" condition is a modification that has developed independently in various taxa of derivate Hygrobatoidea (s.T.), e.g., in Arrenuridae. In these groups, the tibia is expanded and protruded ventrally to oppose the tarsus, permitting the mites to securely grasp and hold slender appendages of prey organisms (Smith & Cook 1991). In the Anisitsiellidae-Limnesiidae complex two very different kinds of pal-

pal shape are found. They are called "anisitsiellid-like" and "mamersopsid-like" palps, as they were once used for distinguishing the families Anisitsiellidae and Mamersopsidae. With the discovery of new species, however, it has become clear that both shapes may appear even in closely related species of a single genus (e.g., *Bandakia*).

The paired chelicerae lie in longitudinal grooves between the palps on the dorsal surface of the gnathosoma. Plesiotypically they consist of a cylindrical basal
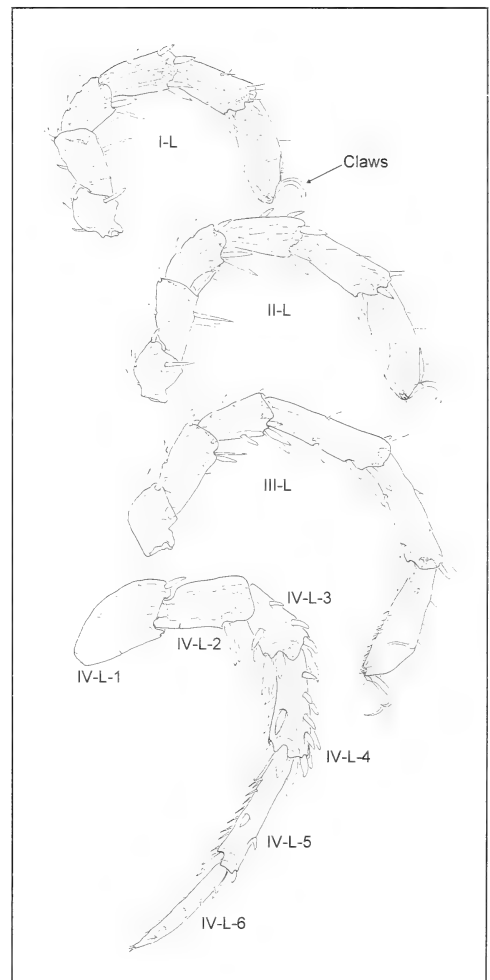
FIG. 15. Morphology of adult Hydrachnellae (*Mamersella thienemanni*). Leg one to leg four. For abbreviations see text [Fig. from slide Ind 93/33 spec. 2].

segment, bearing a movable terminal claw, designed for tearing the integument of prey organisms (Smith & Cook 1991). The pair of chelicerae is plesiotypically separate but fused medially in Limnocharoidea and Eylaoidea. Hydrachnoidea are unique in having unsegmented stiletiform chelicerae.

Idiosoma. Plesiotypically, the idiosoma is mostly unsclerotized, ovoid in outline, and slightly flattened dorsoventrally as in certain extant members of Hydryphantinae, Thyadinae, and Pseudohydryphantinae (Smith & Cook 1991). In the anterodorsal integument are found paired lateral eyes. Plesiotypically one median eye is present. The metameric structures are plesiotypically four pairs of setae on the prodorsum (A1, A2, R1, R2), four pairs of dorsohysterosomal setae (Dh1-Dh4), four pairs of laterohysterosomal setae (Lh1-Lh4), four pairs of ventrohysterosomal setae (Vh1-Vh4), two pairs of setae usually on or near the coxae (Cg2, Cg4), and one pair of setae called

"Ce." Glands are associated with all these setae except R1 and R2. One always finds five slit organs (So 1–5) laterally on the idiosoma. The genital field (comprising the gonopore and plesiotypically three pairs of acetabula and the genital valves) lies ventrally between or posteriorly to the coxae, or secondarily shifted posterior in some taxa (genera of e.g., Aturidae and Unionicolidae). The excretory pore is slit-like and is situated posterior to the genital field.

Legs. Four pairs of legs (I-L, II-L, III-L and IV-L) are inserted laterally on the coxae. They plesiotypically articulate on a ventral major axis and have six movable segments (L-1 to L-6) which articulate to permit ventral flexion. Plesiotypically, the leg tarsi (L-6) bear paired claws terminally. These claws are often reduced in the fourth leg. Setae vary from elongated and hairlike to short and blunt. However, in contrast to the situation in larvae, the adult setae are not yet helpful in elucidating the higher systematics of this group.

2. OBJECTIVES OF THE STUDY

During studies on biogeography and systematics of water mites of the Himalayas, a taxon was detected with characters intermediate between Anisitsiellidae and Limnesiidae, two taxonomically distant families following traditional taxonomics (e.g., Cook 1974). A thorough study of the taxonomical relationship between the two families revealed several similar cases in American forms (e.g., *Rheolimnesia, Siboneyacarus, Mixolimnesia* and *Neomamersa*) and led to the objective of this study: a revision of the family Anisitsiellidae.

Some genera currently placed in the Anisitsiellidae could be more closely related to genera of the Limnesiidae or to other families of the Hygrobatoidea (s.T.), such as Rutripalpidae or some members of the Sperchontidae, than to the remaining genera of their own family. The clarification of the relationship between the taxa of the Anisitsiellidae and certain taxa of other families in the Hygrobatoidea (s.T.), was the main objective of the revision of the 132 species and 31 genera currently placed in the Anisitsiellidae.

In traditional systematics (e.g., Cook 1974) Anisitsiellidae and Limnesiidae are placed in two different superfamilies. Tuzovski (1987) suggests placing them both in the superfamily Hygrobatoidea. Hence, prior to the revision of the Anisitsiellidae, the super-family concept of Tuzovski (1987) is tested. Recent results in this field are compared with those of Tuzovski (1987). A phylogenetic approach to the evolution of Hydrachnellae with a cladistic analysis is undertaken in order to outline the significance of the results on segmental remnants for the definition of the superfamilies.

The position of acetabula and their role in the systematics of Hydrachnellae

The nymphs and adults of many water mite families possess a genital field that contains knobs with an osmoregulatory function, called acetabula (Ac). In adults of anisitsiellid-like species, the acetabula are situated in the soft integument between the movable genital flaps and flanking the gonopore. In limnesiid-like species they are situated on these flaps or their immovable homologs (Fig. 16).

This difference in the position of genital acetabula was used as a character by Viets (1936) in a key to adults, and had a considerable impact on the perception of families and superfamilies in Hydrachnellae. In the dominant taxonomic systems of Viets (1936–56) and Cook (1974), the families Anisitsiellidae and Limnesiidae, as well as the superfamilies Le-
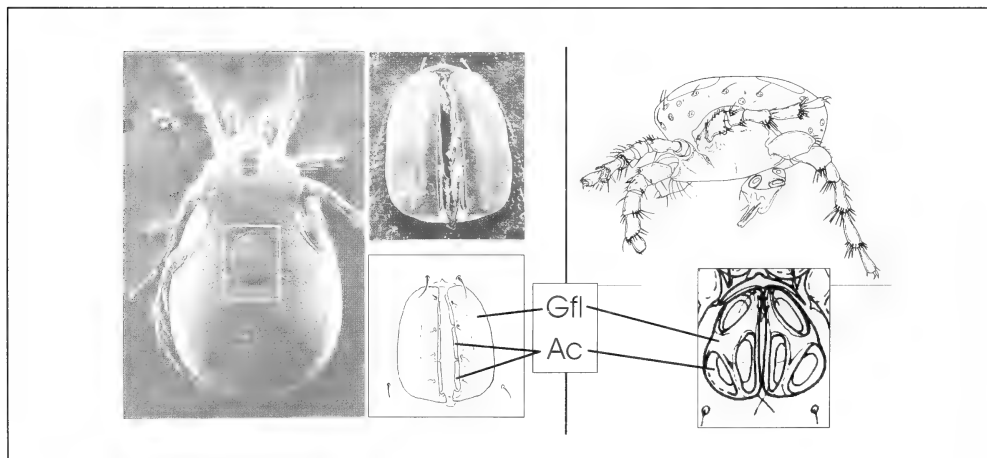
FIG. 16. Position of acetabula in an anisitsiellid-like and a limnesiid-like Hydrachnellae. A "Anisitsiellid-like" mite: *Mahemamersides* sp., male; A1 ventral view, genital field indicated by a frame, A2 detail of genital region with acetabula (Ac) below movable genital flaps (Gfl). B Limnesiid-like mite: *Tyrrellia crenophila*; B1 lateral view of male, genital flaps opened, genital sclerite exposed, B2 detail of genital region: acetabula (Ac) on genital flaps (Gfl) [Figs. A: from Bader (1985), Figs. B: from Cook (1974)].

TABLE 4. The families Anisitsiellidae and Limnesiidae are placed in two different superfamilies (Lebertoidea and Hygrobatoidea) in the systems of Viets (1936, 1956a) and Cook (1974), but in the same superfamily (Hygrobatoidea) in the system of Tuzovski (1987). Different shades of the bars in the left part of the table correspond to the list of families on the right side: all families at the level of a particular shade belong to the same superfamily in the respective systematic concept.

Superfamily-borders in Hydrachnellae as proposed by Viets 1926-56, Cook 1974 and Tuzovski 1987					Families as accepted by Tuzovski 1987

Pontarachnidae
Arrenuridae
Laversiidae
Arenohydracaridae
Hungarohydracaridae
Harpagopalpidae
Athienemanniidae
Acalyptonotidae
Krendowskiidae
Chappuisididae
Bogatiidae
Horroelanidae
Nipponacaridae
Kantacaridae
Uchidastygacaridae
Mideopsidae
Momoniidae
Gretacaridae
Mideidae
Aturidae
Astacocrotonidae
Pionidae
Feltridae
Unionicolidae
Ferradasiidae
Hygrobatidae
Omartacaridae
Limnesiidae
Pontarachnidae
Torrenticolidae
Oxidae
Lebertidae
Anisitsiellidae
Rutripalpidae
Teutoniidae
Sperchontidae
Pseudohydryphantidae
Thermacaridae
Hydrodromidae
Ctenothyadidae
Rhynchohydracaridae
Teratothyadidae
Hydryphantidae
Eupatrellidae
Wandesiidae
Hydrachnidae
Piersigiidae
Eylaidae
Limnocharidae
Hydrovolziidae

Arrenuroidea
Hygrobatoidea
Hygrobatoidea
Lebertoidea

1926	1936	1956	1974	1987
	Viets		Cook	Tuzovski

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bertoidea and Hygrobatoidea, were separated mainly by the dichotome key character "acetabula below movable flaps present? (yes/no)."

In his revision of the Hydrachnellae superfamilies, Tuzovski (1987) discusses all life-stages and many character complexes and arranges the roughly 50 families of Hydrachnellae into 9 superfamilies (Table 4). Tuzovski (1987) merges the Lebertoidea and the Arrenuroidea with the Hygrobatoidea Koch 1842 (Table 4), pointing out that there are striking autapomorphies for the Hygrobatoidea (*sensu* lato) although the differences in the group are difficult to interpret.

Synapomorphies in the larval stage of the Hygrobatoidea (s.T.) include the adaptation of the larvae to hunt preadult instars of their hosts underwater (while most other taxa locate their hosts while running on the water surface), the fusion of basifemur with telofemur, and the reduction of the median eye.

Apart from the arguments presented by Tuzovski (1987), the "*Rheolimnesia* problem" (described below) has already made it clear that the character "position of the genital acetabula in adults" was overestimated in its significance for systematic questions by Viets (1936-56) and Cook (1974).

The Rheolimnesia problem

The *Rheolimnesia* problem arose in 1983. The discovery of the male of *Rheolimnesia tronchoni* made it obvious that the position of the acetabula can show an extreme sexual dimorphism.

In 1953, the females of the species *Rheolimnesia tronchoni* had been described and assigned to the Limnesiidae by Lundblad. The only reason for not putting the new taxon under the Anisitsiellidae was the fact that they possessed acetabula arranged on the surface of movable genital flaps, a character state clearly designating them as members of the Limnesiidae (Fig. 17 b).

However, the *Rheolimnesia tronchoni* males described in Orghidan & Gruia (1983) surprisingly did possess acetabula situated below the movable genital valves (Fig. 17 a), a character state clearly placing them within the Anisitsiellidae. Following current systematics, one would have to assign the two sexes of this species to two different families and – in the systems of Viets (1956) and Cook (1974) – to two different superfamilies.

Other species of the genera *Rheolimnesia* and *Siboneyacarus*, were discovered which displayed the same
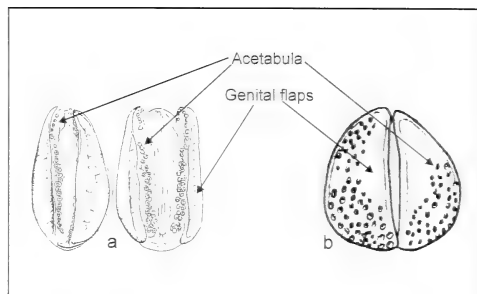
FIG. 17. Position of genital acetabula (Ac) in the species *Rheolimnesia tronchoni*. (a) in males, (b) in females [Fig. a from Orghidan & Gruia (1983); Fig. b from Cook (1974)].

or a similar type of sexual dimorphism. Consequently, the position of acetabula can no longer be accepted as the main and only character for distinguishing the two families and superfamilies.

The revision of the superfamilies undertaken by Tuzovski (1987) solved the contradictions on the superfamily level. Still the question remains: "What is the relationship between the families Anisitsiellidae and Limnesiidae?"

Finding general differences between Anisitsiellidae and Limnesiidae turned out to be difficult. Wiles (1997) shows that a characteristic gland present in the Limnesiidae, known as „Glans Limnesiae," is homologous to a gland found in the very same position in most members of the Anisitsiellidae and certain other closely related families. Other similarities between the Anisitsiellidae and the Limnesiidae include the shape and chaetotaxy of the adult palp and some morphological aspects of the larva.

The Anisitsiellidae are one of the most problematic families of the early derived Hygrobatoidea (s.T.). There are as yet no characters which would allow the definition of the family as a monophylum (Cook 1974). Consequently, some authors called for an adequate revision of the Anisitsiellidae to clarify the relationship of this family to other taxa of the Hygrobatoidea (s.T.), especially the Limnesiidae (Cramer & Smith 1991, Gerecke & Smith 1993).

Questions investigated

The literature on metameric structures in the body wall of the Hydrachnellae (Wiles 1997, Weigmann 2001) is discussed to validate Tuzovski's (1987) new perception of superfamily borders. This is necessary

because the system of Tuzovski (1987) is the only well-founded system in which the two families Anisitsiellidae and Limnesiidae do belong to the same superfamily.

The superfamily Hygrobatoidea (*sensu* Tuzovski) is defined in order to have a basis for the discussion of the relations between Anisitsiellidae and Limnesiidae.

To determine the significance of the above mentioned formulated hypothesis for the definition of the superfamilies, they are tested with a phylogenetic analysis.

The revision of type material of species so far placed under Anisitsiellidae forms the basis for the analysis of taxonomic questions. It includes the description of new taxa of anisitsiellid-like Hydrachnellae, most of them discovered during investigations on the water mite fauna of the Himalayas and the Indian peninsula undertaken in the course of this study.

Among the characters useful for the separation of taxa with the help of comparative morphology, but not documented by many authors, are (1) the organization of the provisory genital field of the nymphal stage, (2) the shape of the chelicera, (3) the shape and chaetotaxy of I-L-6 and IV-L-6, and (4) the organization type of the coxae. Drawings of the relevant features were produced from the available material and compared with the figures already published in order to allow the detection of transformation series in Anisitsiellidae taxa.

The revision of the Anisitsiellidae is restricted to taxonomics. Nevertheless, the main question during the revisionary work was the selection of characters useful for higher systematics (1) in anisitsiellid-like Hydrachnellae, (2) in Limnesiidae and their subfamilies, and (3) in early derived Hygrobatoidea (s.T.).

3. MATERIAL AND METHODS

Material

Material from field collections in India

More than 500 field samples from various parts of India were taken and checked for Hydrachnellae by the author in the years 1989 to 1996. Samples were collected during a project on the ecology of *Eichhornia crassipes* (Panesar 1993), undertaken with a fellowship of the Indo-German exchange programme (Ministry for Human Recourse Development, New Delhi and DAAD, Bonn) and during the course of the Indo-German project "Strengthening of Indian Central and State Pollution Control Boards" (Project Nr. 93.2060.7-01.100 GTZ, Eschborn, Germany) (Panesar 1992; Panesar & Gerecke 1994; Panesar 1995, 1998).

In this study, I refer exclusively to those approximately 40 collections in which water mites of the Anisitsiellidae-Limnesiidae complex were discovered.

List of collections and sampling sites

In the list of collections and sites given below (Table 5), the individual samples are sorted according to the collection date (given as "year, month, day" = yyyy-mm-dd). In cases when more than one collection was made during one day an additional number (_1, _2, _3 ...) was added. In those cases where identification values (ID) have been given to the tube or subsample, these numbers are added in brackets at the end of the code [= ID].

TABLE 5. List of collections from India, and information on the sampling sites.

Code: yyyy-mm-dd_ No. [ID]	Site Country, state, area, location, habitat, height above sea level
1989-12-10 [29;K1]	India, Tamil Nadu, Palni Hills, near Kodaikanal, Bearschola, mountain stream
1989-11-28 [15;K61(2)]	India, Maharashtra, Highway 4 near Kolhapur; irrigation channel, near Panchgangi river; 700 m
1989-11-28 [15;K83]	India, Maharashtra, 180 km south of Pune, between Karad & Kolhapur on Highway 4; Varna river; 700 m
1990-01-17 [K36]	India, Kerala, Trivandrum, Ernakulam Lake, a few yards from the open sea; 5 mNN; from *Eichhornia crassipes*
1990-04-20_1 [52;18/90]	India, U.P.; Garhwal Himalayas, Beyong Ghat, on the road to Kedarnath, 7 km after Gupta Kashi;
1990-04-20_1 [52;8/90]	India, U.P.; Garhwal Himalayas, Beyong Ghat, on the road to Kedarnath, 7 km after Gupta Kashi;
1990-04-20_2 [53(2);37/90]	India, U.P.; Garhwal Himalayas, near Gaurikund, direction Kedarnath, from helocrene near stream; 2,000 m
1990-04-20_3 [54;30/90]	India, U.P.; Garhwal Himalayas; waterfall below Gaurikund; 2,000 m
1990-04-20-4 [55;33/90]	India, U.P.; Garhwal Himalayas; below Gaurikund, 16 km before Gupta Kashi; waterfall; 1,650 m NN
1990-06-12_1 [69;K7]	India, U.P., near Delhi, Ghaziabad, Hindon river, rocky shore (P3) near bridge of National Highway 24; 200 m
1990-06-12_2 [69;K8]	India, U.P., near Delhi, Ghaziabad, Hindon river, rocky shore (P2) near bridge of National Highway 24; 200 m
1990-06-12_3 [69;K9]	India, U.P., near Delhi, Ghaziabad, Hindon river, rocky shore (P2) near bridge of National Highway 24; 200 m
1990-08-22-1 [L3/90]	India, H.P.; Lahul, Sissu Narasari, waterfall on tributary of Chenab; 3,100 m
1990-08-23-2 [L5 G]	India, H.P.; Lahul, on the Manali-Leh road, 13 km after Keylong; rheocrene; 3,300 m
1990-08-23-3 [L6/90]	India, H.P.; Lahul, 15 km after Keylong, on the Manali-Leh road, irrigation system; from roots of macrophytes; 3,300 m
1990-08-23-4 [L10/90]	India, H.P.; Lahul; Manali-Leh road, 5 km north of Rohtang Pass; 3,500 m
1990-08-24 [Solan]	India, H.P. upper Kullu Valley, Solanpur, between Manali and Rohtang on the left side; stream; 2,500 m
1990-09-26 [-350-]	India, U.P., road Delhi-Ghaziabad, ponds in wetland near Hindon, 500 m upstream of National Highway 24; 200 m

TABLE 5. Continued.

Code: yyyy-mm-dd_ No. [ID]	Site Country, state, area, location, habitat, height above sea level
1990-09-30 [-65-]	India, U.P., road Delhi-Ghaziabad, ponds in wetland near Hindon, 500 m upstream of bridge of National Highway 24; 200 m
1990-12-31 [Ec(3)]	India, U.P., road Delhi-Ghaziabad, pond with *Eichhornia*, 500 m upstream of bridge of National Highway 24; 200 m
1993-05-28 [2/93]	India, Darjeeling; near Rimbik; 2 km trek towards Bansbotey, (below! path Rimbik-Sandakphu); rocky stream; 2,200 m
1993-05-30_1 [7/93]	India, Darjeeling; 2 ? h trek from Sandakphu towards Sabarkum-Phalut; spring stream, east of path in side valley; 3,500 m
1993-05-30_2 [8/93]	India, Darjeeling; 4 h trek from Sandakphu to Sabarkum-Phalut; 2 h before Molley; mountain stream; mosses; 3,300 m
1993-05-30_3 [9/93]	India, Darjeeling; 5 h trek from Sandakphu to Sabarkum-Phalut; 1 h before Molley; mountain stream; detritus; 3,200 m
1993-05-31_2 [13/93]	India, Darjeeling; 1.2 km trek from Phalut to Gorkhey, bamboo forest on right hand side; seepage area near stream; 3,450 m
1993-05-31_3 [14/93]	India, Darjeeling; 1.2 km trek from Phalut to Gorkhey, bamboo forest on right hand side; mountain stream 3,450 m
1993-06-01 [16/93]	India, Darjeeling; after 500 m from Gurkey to Phalut, drinking ditch for cattle; detritus, sand, macrophytes; 2,500 m
1993-06-02_1 [21/93]	India, Darjeeling; 2 km trek from Gorkey to Ramam-Rimbik, forest stream at bridge; from mosses; 2,200 m
1993-06-02_2 [22/93]	India, Darjeeling; 3 km trek from Gorkey to Ramam-Rimbik, forest stream at bridge; from mosses; 2,200 m
1993-06-03_1 [23/93]	India, Darjeeling; on path from Gorkey to Ramam-Rimbik, steep stream; mosses, detritus; 2,510 m
1993-06-03-4 [26/93]	India, Darjeeling; on path from Gorkey to Ramam-Rimbik, small stream; 2,200 m
1993-06-10 [34/93]	India, U.P., Garhwal Himalaya, north of Rishikesh, 27 km after Narendra Nagar; waterfall (carbonate-rich); 1,200 m
1995-07-24 [95/58]	India, H.P., Kullu Valley, Kunoi Nala, between Sujla and Kakhnal; waterfall with mosses; 1,800 m
1995-06-11 ['95/18M]	India, H.P., Kullu Valley, between Sujla and Kakhnal, small waterfall with mosses, 1,800 m
1995-06-16 ['95/43]	India, H.P., Kullu Valley, Kunoi Nala, waterfall with mosses, 25 min trek upstream of Kakhnal, 2,000 m
1995-06-26 ['95/82]	India, H.P., Kullu Valley, Kunoi Nala, "P2", cascade with mosses, approx. 30 min trek upstream of Kakhnal, 2,000 m
1995-07-06 ['95/122]	India, H.P., Kullu Valley, Karol Nala, 4 h trek from Naggar/Nishalla towards north; 2,200 m
1995-07-10 ['95/147]	India, H.P., Kullu Valley, Kunoi Nala, headwaters/spring area, 3,600 m
1995-07-13 ['95/170]	India, H.P., Kullu Valley, Kunoi Nala, 30 min trek upstream from Kakhnal; mosses from pool, 2,000 m
1995-08-13 ['95/253-6]	India, H.P., Lahul, by jeep 1-2 h before Baralacha Pass, stream joining a small lake; 3,800 m
1996-06-14_1 ['96/190]	India, H.P., Kullu Valley; Naggar Nala; drift 08:10-08:20h; 1,800 m
1996-06-14_2 ['96/191]	India, H.P., Kullu Valley; Naggar Nala; drift 08:10-08:20h; 1,800 m
1996-06-14_3 [96/192]	India, H.P., Kullu Valley, Naggar Nala; at highway between Kamsari and Naggar, 500m upstream; drift; 1,800 m
1996-06-16 ['96/222]	India, H.P., Kullu Valley; Naggar Nala; drift; 1,800 m
1996-06-16 ['96/236]	India, H.P., Kullu Valley; Naggar Nala; drift; 1,800 m
1996-06-16 ['96/247]	India, H.P., Kullu Valley; Naggar Nala; drift; 1,800 m

Example: "1990-06-12_2 [69;K8]" is the code for the second sample taken on June 12, 1990, with identification values "69" and "K8."

Material from museums and private collections

Type material and other identified material of Anisitsiellidae examined for this study was obtained from the following collections:

- coll. Viets, Senckenberg Museum Frankfurt am Main, Deutschland (SMF),
- coll. Bader, Naturhistorisches Museum Basel, Schweiz (NMB),
- coll. Schwoerbel & Sepasgozarian material from the NMB,
- coll. Lundblad, Swedish Museum of Natural History, Stockholm, Sweden (SMH),
- coll. Sokolow, Museum of Nat. Hist., St. Petersburg, Russia (NHP),
- private collection of Gerecke, Tübingen, Deutschland (CRG); and
- private collection of Panesar, Freiburg, Deutschland (CAP).

During the investigations in the NMB, unpublished figures of late authors (Halik, Bader) were discovered for some genera (e.g., *Hydrobaumia, Mahemamersides*). They are published here because of their relevance for the analysis.

Methods

Sampling methods, conservation and preparation

The "Thienemann net" is an ideal piece of equipment for qualitative collections of Hydrachnellae. It is a combination of two nets with different mesh sizes: a net with a mesh size of 2 mm (metal sieve) is put into the mouth of a net with a mesh size of 300 µm. In stagnant or slowly flowing waters, the "Thienemann net" is moved through macrophytes or substrates. In running waters, the substrate is disturbed just upstream of the mouth of the net and taken into the net by the water current. The double-net is rinsed with water after the collection so that all particles smaller than 2 mm are washed through the upper net into the lower net. Both fractions of the sample are put in two separate trays. After some time, the water mites run on top of the substrate or on the white bottom of the trays and are sorted out with soft forceps. Drift samples sometimes yield remarkable specimens of Hydrachnellae not found with other sampling devices at the selected sampling site. For this study, a drift net (Schwoerbel 1994) with a mouth opening of 10 x 100 cm and mesh size of 300 µm was used. Each sample was exposed for 10 minutes in the mountain stream under investigation; this exposure was repeated every hour during 1–3 days. Water mites from the

drift samples were sorted out as given above. Out of more than 100 drift samples, only those two samples containing Hydrachnellae of the Anisitsiellidae-Limnesiidae complex are quoted in the above list of collections.

Mites were conserved in KOENIKE′s solution (Schwoerbel 1994). Slides and preparations were made with HOYERS fluid or EUPARAL. Mouthparts, legs or other body parts were dissected under a stereo microscope (Wild Typ M5) and positioned as given by Gerecke (1991).

Drawings, EM-photographs and measurements

Ink drawings were made with the help of a "Leitz Laborlux K" microscope. EM-photographs were provided by TOM GOLDSCHMIDT (University of Münster, Germany). The following figure (Fig. 18) shows the regions of the water mite idiosoma and palp from where measurements were taken.

Parsimony calculation

The program HENNIG86 (Farris 1988) was used to produce a cladogram for the superfamilies of the Hydrachnellae. The characters selected for the analysis are morphological features of the larvae as given by Tuzovski (1987), characters of the adults (Cook 1974, Wiles 1997), and data on apotypic behavior of larvae (Smith & Oliver 1986). The characters are discussed in detail in Chapter 4 "What are Hygrobatoidea s.T.?"
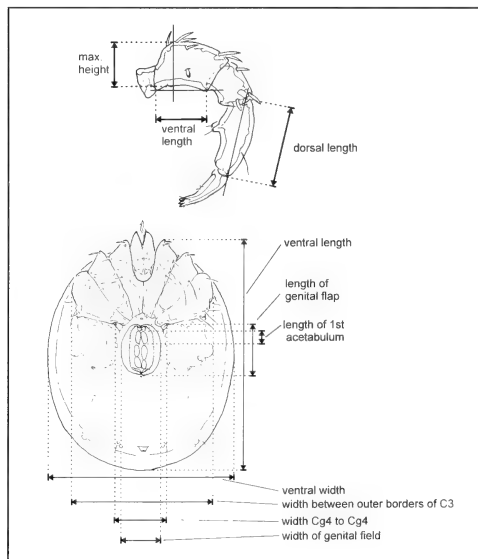
FIG. 18. Measuring distances of water mite body parts (*Bandakiopsis* sp.). Top: palpus. Bottom: VS.

4. WHAT ARE HYGROBATOIDEA "*SENSU* TUZOVSKI 1987?"

Harvey (1998) suggests excluding the family Sperchontidae from the Lebertoidea (sensu Cook 1974) and raising them to superfamily status. He gives no autapomorphy and states that there are only plesiomorphies shared by the members of the newly suggested superfamily. In the same work he suggests shifting the Limnesiidae to the Lebertoidea (*sensu* Cook 1974). He suggests treating the position of the "Glans Limnesiae" (= Coxoglandulare 4 = Cg4) on coxa 3 (= C3) or C2 as the synapomorphic character state for the Lebertoidea. However, as shown by Wiles (1997), this gland is present in different positions (including on C3 or C2) in *Albia* as well as in a wide range of taxa from all the three superfamilies Lebertoidea, Hygrobatoidea (sensu Cook 1974) and Arrenuroidea.

Smith & Cook (1991) conclude that the three superfamilies Lebertoidea, Hygrobatoidea (sensu Cook 1974) and Arrenuroidea, as well as the superfamily Hydryphantoidea, are all either para- or polyphyletic. Other authors (e.g., Smith & Oliver 1986, B.P. Smith 1988) suggest that the families comprise various clades which derived independently from hydryphantoid-like stock, as their larvae have independently developed apotypic associations with Diptera, Trichoptera, Coleoptera and Odonata.

There is also the tendency to lump superfamilies together in case no convincing autapomorphies are available, instead of raising new superfamilies.

Hardly noticed is the [Russian] publication by Tuzovski (1987); in his revision of Hydrachnellae superfamilies, he merges the two superfamilies Lebertoidea and Arrenuroidea with the Hygrobatoidea Koch 1842. The only taxon which Tuzovski (1983) excluded from the group is the family Pontarachnidae, placed in the separate superfamily Pontarachnoidea Tuzovski, 1983.

The superfamily concept of Tuzovski (1987) is mainly based on alterations in the idiosomal chaetom and glands of the Hydrachnellae. Tuzovski (1987) does not see enough differences among the 35 families of the Hygrobatoidea (s.T.) to justify more than a single superfamily (cf. Table 4).

The taxonomic system of Tuzovski (1987) is the only well-founded system in which Anisitsiellidae and Limnesiidae are both placed under the same superfamily Hygrobatoidea Koch, 1842 (*sensu* Tuzovski 1987). Hence, prior to the discussion of the relationship between the families Anisitsiellidae and Limne-siidae, a discussion on the superfamily boundaries of the Hygrobatoidea (s.T.) is needed.

Discussion of segmental remnants

Tuzovski (1987) uses as a strong argument the apomorphic reductions from the original set of segmental remnants. At the same time he uses a segmentation concept which clearly differs from the one used by Wiles (1997).

The term "segmental remnants" refers to the metameric pairs of glands, proprioreceptors, and setae which reflect the ancestral segmentation of the water mite body. In publications on Hydrachnellae, different concepts of the water mite body are suggested and different nomenclatures are used for segmental remnants in these concepts. Wiles (1997) made an effort to compare and homologize the terminologies used by water mite researchers without discussing the rival concepts.

In the following the results of Wiles (1997) and the other current "western" concepts on body plans – as reviewed by Weigmann (2001) – are compared with the concept of Tuzovski (1987).

The concept of Wiles (1997)

Wiles (1997) mainly follows Grandjean (1970) and Coineau (1974), who suggest that dorsal elements of the first segments have encroached above those ventral elements of the podosoma that support legs I and II, while dorsal elements of the ophistosoma have encroached over the ventral elements supporting legs III and IV. Consequently, all segments which support legs are only visible in their ventral parts (Fig. 19).
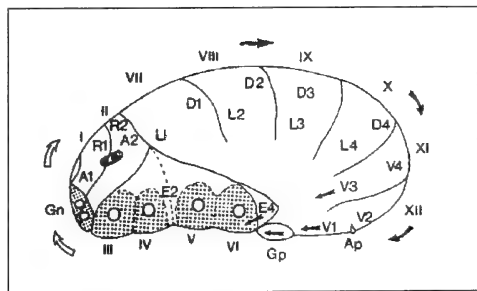
FIG. 19. Ground plan of the Hydrachnellae (adults) as suggested by Wiles (1997) (for abbreviations see text).

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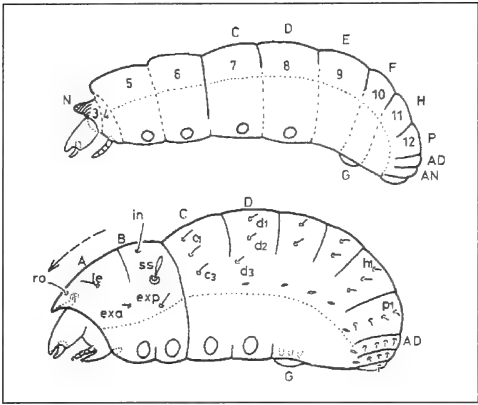
FIG. 20. Ground plan of segmentation of a hypothetical ancestor. Top: archetype of acariform mite. Bottom: actinedid mite [adapted from Weigmann (2001)].

According to Wiles (1997), in adult Hydrachnellae there are 4 pairs of propodosomal setae, A1, A2 and R1, R2, one pair of setae belonging to the segments each carrying the coxa 2 and coxa 4 (E2, E4), while the other two (E1, E3) are always reduced, and 12 pairs of hysterosomal setae (D1-D4 for dorsal setae, L1-L4 for lateral setae, and V1-V4 for ventral setae). Metameric structures of the body wall are tentatively related to certain segments as given in Fig. 19. They are not related through their names to certain segments (e.g., C1, C2 for setae on segment C) instead they are simply numbered from anterior to posterior.

Wiles (1997) accepts the system of superfamilies suggested by Cook (1974) without changes. He does

not discuss the potential use of chaetotaxy for the definition of superfamilies.

The concept of Tuzovski (1987)

The system of Tuzovski (1987) (Fig. 21) is similar to the one suggested by Grandjean (1934) and Weigmann (2001). Here, neither anterior nor posterior segments encroach over podosomal segments. Weigmann (2001) suggests applying a modified version of the concept presented by Grandjean (1934) for the following reasons: (1) there is no argument available why dorsal parts of elements should encroach over podosomal elements and (2) that the position of the segmental remnants does not promote such a theory.

According to Tuzovski (1987), in adult Hydrachnellae the two frontal segments (see Fig. 21 and Table 6) carry one pair of setae each (Fch, Fp), the following eight segments (V, O, H, Sc, L, S, C, P) carry an medial and an lateral seta (e.g., Vi, Ve), while segment "H" alone carries a third seta (Hv). Five segments (O to S) carry a pair of slit organs. Different setae are reduced in different active life stages and superfamilies, and their presence or absence among Hydrachnellae is stable enough to be used as apomorphic character states for the definition of several superfamilies. In adults, e.g., the seta "Ce" and ist corresponding gland are reduced in all superfamilies of Hydrachnellae, with the exception of Limnocharoidea and Pontarachnoidea.

In the concept of Tuzovski (1987), setae and glandularia are related to certain segments through their name - e.g., "Si" and "Se" are names for setae on segment "S."

Discussion of adults. Although Wiles (1997) and Tuzovski (1987) differ in their view of the water mite

TABLE 6. Scheme of segmentation, setae and slit organs in water mites (after Tuzovski 1987) (for abbreviations see text).

Idiosoma Segment	I.	II.	III.	IV.	V.	VI.	VIII.	IX.	X.	XI.	n
Internal setae	Fch	Fp	Vi	Oi	Hi	Sci	Li	Si	Ci	Pi	Ai
Slit organs				i1	i2	i3	i4	i5			
External setae			Ve	Oe	He	Sce	Le	Se	Ce	Pe	Ae
Humeral setae					Hv						
Genital acetabula							g1	g2	g3		
Coxae & excret. pore		Cx1	Cx2	Cx3	Cx4					ExP.	

The two pairs of anal setae (= Ai, Ae) are present in larval stages only. The 3rd acetabulum (= g3) is absent in larva and nymphs but present in all adults. The structures Ve, g1–g3 and Cx4 are absent in all larva.
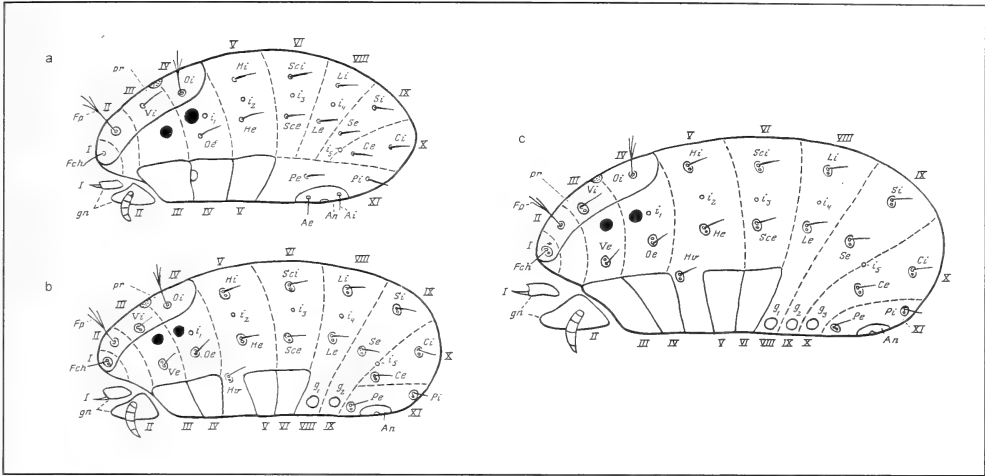
FIG. 21. Ground plan of the Hydrachnellae as suggested by Tuzovski (1987). (a) larva, (b) deutonymph, (c) adult (for abbreviations see text).

TABLE 7a. Nomenclatures of Tuzovski (1987), Wiles (1997), and Weigmann (in press) for setal pairs in the idiosoma body wall. Names suggested as homologs are placed in the same line. The tables follow either Tuzovski (a1) or Wiles (b1 – see next page) regarding the segment numbers. Abbreviations suggested in this study are given in (a2) and (b2 – see next page).

(a1)   (a2)

Seg. No.	Weigmann (in press)	Seg. No.	Tuzovski (1987)	Seg. No.	Wiles (1997)	suggested abbrev.:
V.	A ro	I.	Fch	I.	A1	A1
V.	A le	II.	Fp	II.	R1	R1
VI.	B in	III.	Vi	II.	A2	A2
??	exa	III.	Ve	VII.	L1	Lh1
VI.	B ss	IV.	Oi	I.	R2	R2
VI.	exp	IV.	Oe	VIII.	L2	Lh2
VII.	C1	V.	Hi	VII.	D1	Dh1
VII.	C2	V.	He	IX.	L3	Lh3
VII.	C3	V.	Hv	IV.	E2	Cg2
VIII.	D1	VI.	Sci	VIII.	D2	Dh2
VIII.	D3	VI.	Sce	X.	L4	Lh4
IX.	E1	VIII.	Li	IX.	D3	Dh3
IX.	E2	VIII.	Le	XI.	V3	Vh3
X.	F1	IX.	Si	X.	D4	Dh4
X.	F2	IX.	Se	XI.	V4	Vh4
XI.	H1	X.	Ci	XII.	V2	Vh2
XI.	H2	X.	Ce	???	???	"Ce"
XII.	P1	XI.	Pi	XII.	V1	Vh1
XII.	P2	XI.	Pe	VI.	E4	Cg4
An	A1	An	Ai	An	Exp 1	An1
An	A2	An	Ae	An	Exp 2	An2

TABLE 7b. Part b of this table is identical with Tab. 7a regarding the contents. However, in part b the abbreviations are given according to the segment numbers of Wiles (1997) and in part a they follow the segment numbers of Tuzovski (1987)

(b1)   (b2)

Seg. No.	Wiles (1997)	Seg. No.	Tuzovski (1987)	suggested abbrev.:
I.	A1	I.	Fch	A1
I.	R2	IV.	Oi	R2
II.	A2	III.	Vi	A2
II.	R1	II.	Fp	R1
IV.	E2	V.	Hv	Cg2
VI.	E4	XI.	Pe	Cg4
VII.	D1	V.	Hi	Dh1
VII.	L1	III.	Ve	Lh1
VIII.	D2	VI.	Sci	Dh2
VIII.	L2	IV.	Oe	Lh2
IX.	D3	VIII.	Li	Dh3
IX.	L3	V.	He	Lh3
X.	D4	IV.	Si	Dh4
X.	L4	VI.	Sce	Lh4
XI.	V3	VIII.	Le	Vh3
XI.	V4	IX.	Se	Vh2
???	???	X.	Ce	"Ce"
XII.	V1	XI.	Pi	Vh1
XII.	V2	X.	Ci	Cg4
An	Exp 1	An	Ai	Ex1
An	Exp 2	An	Ae	Ex2

body, they come to similar results regarding the total number and position of setae and glandularia. They show consistency in their systems in the sense that a structure called "E2" in Wiles system will be named "Hv" in Tuzovski's.

Table 7 suggests homologies between the systems of Tuzovski (1987), Wiles (1997), and Weigmann (2001).

Wiles (1997) counts 18 pairs of idiosomal setae, corresponding to 16 pairs of glandularia, as maximum numbers for adults. However, most of the species included in his investigation belong to the Hygrobatoidea (s. T.). In his comparative study, Tuzovski (1987) includes several early derivate taxa not covered by Wiles (1997). He finds the maximum numbers of 19 pairs of idiosomal setae corresponding to 17 pairs of glandularia in members of the superfamilies Pontarachnoidea and Limnocharoidea (sensu Tuzovski).

Table 7 and Table 8 show that the results of Wiles (1997) and Tuzovski (1987) agree with each other regarding the sets of idiosomal setae. Apart from their incongruent concept of segmentation, the main difference is that Tuzovski (1987) investigated a number of taxa and life stages not covered in Wiles (1997) and is therefore able to include a further setal pair "Ce" and its glandularia into his system which he found to be present in some early derived families of the Hydrachnellae only.

The existence of glandulare "Ce" in Limnocharoidea and in Pontarachnoidea, as depicted by Tuzovski (1987), contradicts the concept of Wiles (1997), which

TABLE 8. Reduction of idiosomal setae in superfamilies of the Hydrachnellae (adults). " – " = seta always reduced. "(–)" = seta sometimes reduced "n." = no data. " p " = seta present. "?" no clear indication which setae is reduced. [Data from Tuzovski (1987) and Wiles (1997)].

Superfamily	m of setal pairs in the idiosoma wall according to:		reduced setal pairs and their individual names according to Wiles / Tuzovski:					
	Wiles	Tuzovski	L1/Ve	V4/Se	E2/Hv	?/Ce	E4/Pe	V1/Pi
1. Hydrovolzioidea	17	17	?/ –				–/–	?/p
2. Eylaoidea	no data	16	n./–	n./–			n./–	
3. Piersigioidea	no data	16	n./–			n./–	n./–	
4. Limnocharoidea	no data	19						
5. Hydrachnoidea	18	18					–/–	
6. Wandesioidea	no data	18 - 17					n./–	n./(–)
7. Hydryphantoidea	18	18					–/–	
8. Hygrobatoidea	18 - 17	18 - 17					(–)/(–)	
9. Pontarachnoidea	no data	19 - 18						n./(–)

TABLE 9. Chaetom of the superfamilies of the Hydrachnellae (after Tuzovski 1987). The first value of a pair "x/y" refers to the larval stage and the second value to nymphs and adults; e.g., "2/1" means the segment carries 2 pairs of setae in larvae and 1 pair in nymphs and adults. (**Bold** numbers indicate the character states used in the cladistic analysis below.).

Idiosomal segment	I.	II.	III.	IV.	V.	VI.	VIII.	IX.	X.	XI.	A
Segment letter	Fch	Fp	V	O	H	Sc	L	S	C	P	A
Superfamily		Protero	soma					Hysterosoma			
1. Pontarachnoidea	?/1	?/1	?/2	?/2	?/3	?/2	?/2	?/2	?/2	?/1-2	?/0
2. Limnocharoidea	1/1	1/1	1/2	2/2	2/3	2/2	2/2	2/2	1/2	1/2	**1**/0
3. Eylaioidea	1/1	1/1	1/**1**	2/2	2/3	2/2	2/2	2/**1**	1/**1**	1/2	**1**/0
4. Piersigioidea	1/1	1/1	1/**1**	2/2	2/**2**	2/2	2/2	2/2	1/**1**	1/2	**1**/0
5. Hydrovolzioidea	1/1	1/1	1/**1**	**1**/2	2/3	2/2	2/2	2/2	1/**1**	1/2	**1**/0
6. Hydrachnoidea	1/1	1/1	1/2	2/2	2/3	2/2	2/2	2/2	1/**1**	1/2	**0**/0
7. Wandesioidea	1/1	1/1	**2**/2	2/2	2/3	2/2	2/2	2/2	1/**1**	1/1-2	2/0
8. Hygrobatoidea	1/1	1/1	1/2	2/2	2/3	2/2	2/2	2/2	1/**1**	**2**/1-2	2/0
9. Hydryphantoidea	1/1	1/1	1/2	2/2	2/3	2/2	2/2	2/2	1/**1**	**2**/2	2/0

Column header note: "No. of setal pairs present per idiosomal segment in: larva / nymphs and adults"

suggests the presence of not more than two setal pairs on one hysterosomal segment. Wiles (1997) confirms that seta E4 (= Pe = Cg4) is found in various positions in different taxa, from posterior to coxa 4, as in some Hydryphantidae, to the anterior edge of coxa 1, as in some Torrenticolidae. It seems that in the latter cases Tuzovski (1987) has missed this glandulare.

Discussion of nymphs and larvae. Tuzovksi (1987) compared the metameric structures not only in adults but also in nymphs and larvae of all Hydrachnellae superfamilies.

As a result he found that larvae show the same basic pattern of setal pairs as adults, but different pairs of the basic chaetom may be reduced in both the larval and the adult stage. The investigations into the reduction of setal pairs in nymphs showed that nymphs exhibit the same basic pattern of setal pairs and that a setal pair reduced in the nymphal stage will be also reduced in the adult stage. Table 9 gives an overview of the superfamilies and their differing sets of setae per segment in larvae on the one hand and nymphs and adults on the other.

Conclusion

The most clear-cut theory on segmentation applied to Hydrachnellae is the above discussed concept suggested by Weigmann (2001), which is quite similar to that of Tuzovski (1987).

Differences between the concepts of Tuzovski (1987) and Weigmann (2001) include:

(1) Tuzovski depicts a proterosoma with segments 1 to 4, while in Weigmann segments 1 and 2 are fused into the region of the "naso" and segments 3 to 6 form the proterosoma.

(2) Segment 7 is completely reduced in Tuzovski's concept, but in Weigmann's it forms the first segment of the hysterosoma.

(3) The genital porus and the three plesiomorphic acetabula of the adult genital field are confined to segment 10 by Weigmann, while Tuzovski suggests that the three segments posterior to the fourth coxae possess one pair of acetablula each.

The system of Tuzovski (1987) is the most precise one for denoting individual setae in Hydrachnellae, as setal names refer to particular segments, e.g., "Ve" is the pair of lateral setae referring to segment "V." Not relating the setae by name to certain segments makes it difficult to compare the sets of setae in different taxa. If in the system of Wiles (1997) seta "L1" (= Ve) is absent, seta "L2" (= Oe), which refers to segment "O," may get the wrong name "L1." Thus, the name "L1" may refer to two different setae which are a segmental remnant either to segment "V" or to segment "O" and which are not homologous.

The comparison of the different concepts discussed above can be summarized in four points:

(1) It is possible to homologize terms used by Tuzovski (1987), Wiles (1997), and Weigmann (2001) (see Table 7).

(2) Several taxa with apomorphic and plesiomorphic sets of segmental remnants were not investigated by Wiles (1997) (see Table 8).

(3) The concept of the Hygrobatoidea (s.T.) is partly based on the uniform set of segmental remnants in all life stages (Table 9) of all families included in this superfamily. The results of Wiles (1997) underline the results of Tuzovski (1987) on the set of segmental remnants in Hygrobatoidea (s.T.). However, the number of investigated species is still to small to finally conclude if the distribution pattern of setae and glandularia is a sufficiently stable character among Hydrachnellae, to define taxa on the family or superfamily level.

(4) The system proposed by Tuzovski (1987) has the advantage of being universally applicable to all active stages of water mites, while "western" systems use a different terminology for homologous structures at different stages.

Suggested terms for metameric structures

"Western" authors are more familiar with the terms suggested by Wiles (1997). In the following text I therefore use a modified form of this nomenclature. I propose to use the terms from Tuzovski (1987) to denote individual setae in those cases where it is difficult to be precise in the terminology of Wiles (1997). I agree with Wiles (1997) and Tuzovski (1987) that homologous setae in larva, nymphs and adults should be given the same name.

I suggest the following changes for terms used by Wiles (1997):

(1) To avoid confusion with the abbreviations for hysterosomal setae of Weigmann (2001), the setae termed D1-4 and V1-4 by Wiles (1997) should be abbreviated as Dh1-4 and Vh1-4. Similarly I suggest useing the abbreviations Lh1–Lh4 for the laterohysterosomal (or anterior four pairs of lateral somatic) setae in larval, nymphal and adult stages

(2) Setae of the excretory pore plate (= anal setae) present in the larval stage should be abbreviated Ex1, Ex2 to avoid confusion with abbreviations for the hysterosomal setae of Weigmann (2001) and the prodorsum setae A1, A2 in works by Wiles, Cook, and Smith.

(3) Abbreviations E2, E4, suggested by Wiles for coxoglandularia, overlap with larval terms used for anal setae in works such as those of Prasad, Cook, and Smith. I suggest useing Cg2 and Cg4 for coxoglandularia 2 and 4.

Tuzovski (1987) uses a formula which gives the total number of setae per segment, from anterior to posterior (e.g., 2-2-4-4-6-4-4-4-2-4-0 for adult Hygrobatoidea (s.T.)). This formula is used for descriptions of superfamilies in the present study. Alterations to this formula are included in a phylogenetic approach to the superfamily concept of Tuzovski (1987) presented in the following chapter.

Testing the superfamily concept of Tuzovski (1987) with a phylogenetic approach

Larval morphology has been extremely valuable in understanding relationships among members of the Parasitengona (e.g., Welbourn 1991). It also appears to be more conservative than adult morphology in Hydrachnellae. With his revision of the superfamilies of the Hydrachnellae, Tuzovski (1987) provides a database for segmental remnants in all active life stages of the Hydrachnellae, including the larva. A comparison of the results of Tuzovski (1987) with those of Wiles (1997) and Weigmann (2001) shows that the latter authors confirm the approach of Tuzovski (1987), and that alterations in the idiosomal chaetom and in the glandularia system are quite conservative in Hydrachnellae as well. Hence it seems justified to include changes in the idiosomal chaetom and glandularia set in the characters used for a parsimony calculation.

Although larval characters are extensively discussed in interpretations of evolutionary trends among higher taxa in Hydrachnellae (Tuzovski 1987, Smith & Cook 1991, Harvey 1998), no publication has so far used a parsimony analysis to look at the superfamilies of the Hydrachnellae from a phylogenetic point of view.

The cladogram for the superfamilies of the Hydrachnellae, shown in Fig. 22, is the product of a cladistic analysis calculated with HENNIG86 (Farris 1988), based mainly on the characters suggested by Tuzovski (1987) and with superfamily Hydryphantoidea as outgroup:

1 = Presence of setal pairs on segment P in larvae [0 = two pairs present; 1 = one pair reduced]

2 = Presence of setal pairs on segment A in larvae [0 = two pairs present; 1 = one pair reduced; 2 = both pairs reduced]

3 = Presence of setal pair "Ve" in nymphs and adults [0 = present; 1 = absent]

4 = Mouth opening surrounded by a large circular membranous fringe (adults)
[0 = absent; 1 = present]

5 = Soft bodied, but eyes incorporated into a median anterior sclerite (adults)
[0 = absent; 1 = present]

6 = Larva locates prospective hosts as prepupa or pupa underwater
[0 = no; 1 = yes]

7 = Body soft and elongated, worm-like (adults)
[0 = no; 1 = yes]

8 = Presence of setal pairs on segment V in larva
[0 = both pairs present; 1 = one pair reduced]

9 = Presence of setal pairs on segment O in larva
[0 = both pairs present; 1 = one pair reduced]

10 = Presence of setal pair "Se" in nymphs and adults
[0 = present; 1 = reduced]

11 = Presence of setal pair "Ce" in nymphs and adults
[0 = present; 1 = reduced]

The distribution of the above character states among the superfamilies is shown in the following table.

TABLE 10. Character set used in the phylogenetic analysis for superfamilies of the Hydrachnellae. Discussion of the characters in the text.

	Characters										
	1	2	3	4	5	6	7	8	9	10	11
Hydryphantoidea*	0	0	0	0	0	0	0	1	0	0	1
Hygrobatoidea	0	0	0	0	0	1	0	1	0	0	1
Wandesioidea	1	0	0	0	0	0	1	0	0	0	1
Hydrachnoidea	1	2	0	0	0	0	0	1	0	0	1
Hydrovolzioidea	1	1	1	0	0	0	0	1	1	0	1
Piersigioidea	1	1	1	1	0	0	0	1	0	0	1
Eylaioidea	1	1	1	1	1	0	0	1	0	1	1
Limnocharoidea	1	1	0	1	1	0	0	1	0	0	0

* = superfamily Hydryphantoidea is selected as outgroup.

Apart from the results concerning the segmental remnants only a few well known morphological and behavioral features of the superfamilies have been included in the data set. Out of the 11 characters used for the phylogenetic analysis, 4 refer to reductions of setal pairs in the larval stage, 4 refer to the reduction of setal pairs in nymphs and adults, 3 refer to morphological characters of the adults, and one refers to behavior of the larva. The predominantly marine Pon-
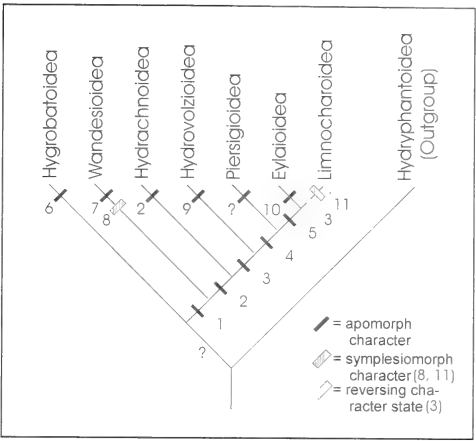
FIG. 22. Cladogram for the superfamilies of the Hydrachnellae. Length = 13; Ci = 92; Ri = 87. Characters 1–11 are described in the text and Tab. 11.

tarachnoidea are not included because their larvae are unknown and possibly reduced.

The interpretation that Hydrachnellae derived from an ancestral terrestrial Parasitengona that may have resembled certain soft-bodied extant Hydryphantoidea is suggested by various authors (Wiggins et al. 1980, Smith & Oliver 1986). So far there are many symplesiomorphic character states shared by the Hydryphantoidea, but no convincing autapomorphic character state for the superfamily is known. Hydryphantoidea are therefore selected as outgroup.

The cladogram produced with HENNIG 86 (Farris 1988), using Hydryphantoidea as outgroup, places the superfamilies as:

(Hydryphantoidea (Hygrobatoidea (Wandesioidea (Hydrachnoidea (Hydrovolzioidea (Piersigioidea (Eylaioidea Limnocharoidea)))))))

(Length = 13; Ci = 92; Ri = 87)

The analysis of the above data set results in a single shortest tree with a length of 13 steps (total number of character-state changes necessary to support the relationship of the taxa in a tree). The relative amount of homoplasy is high [consistency index (Ci) = 92, retention index (Ri) = 87].

Hence, the phylogentic analysis supports the hypothesis of Tuzovski (1987) that the reductions from the basic set of segmental remnants in the active life stages, larvae, nymphs, and adults, are a useful character complex for the higher systematics of the more than 6000 species of Hydrachnellae.

As a result of the above considerations and of the phylogenetic analysis, it is suggested that Tuzovski (1987) is followed and that Lebertoidea and Arrenuroidea (*sensu* Cook 1974) are treat as junior synonyms of the Hygrobatoidea Koch, 1842.

Consequences for the concept of Hygrobatoidea

The investigations of Tuzovski (1987) and of Wiles (1997) show that all members of the superfamilies Hydryphantoidea and Hygrobatoidea (s.T.) exhibit the same set of setal pairs: total number of setae per segment from anterior to posterior is 2-2-2-4-4-4-4-4-2-4-4 in larvae and 2-2-4-4-6-4-4-4-2-4-0 in adults.

Regarding the set of segmental remnants, a general difference between the concepts suggested by other authors (e.g., Smith & Cook 1991, Harvey 1998, Witte 1999) and the cladogram based on the superfamily concept of Tuzovski (1987) is that the so called "modern" or "higher" water mites show a more plesiomorph "old-fashioned" set of characters, while the taxa commonly treated as early derivative – like Hydrovolzioidea – show many apomorphic changes from the original set of segmental remnants. This difference has already been noted by Tuzovski (1987) and is well visible in the data matrix (Table 10) and the resulting cladogram (Fig. 22).

The features for which in the literature water mites are called "modern" or "old-fashioned" are not related to their set of segmental remnants but to other characters related to apotypic behaviors of larva and adults (e.g., rapid swimming).

Synapomorphic character states of the Hygrobatoidea (s.T.). While in all other Hydrachnellae in the larval stage the (preanal) segment P carries one pair of setae only, in Hydryphantoidea and Hygrobatoidea it shows the plesiomorphic situation with a total of two setal pairs. The possession of two pairs of setae on segment P is a symplesiomorphy of the larvae of Hygrobatoidea. Having one setal pair on segment P reduced is a synapomorphy of the larvae of all superfamilies except Hygrobatoidea. The presence of two pairs of setae on the (last) anal segment A in the larval stage is a symplesiomorphy shared by Hygrobatoidea, Hydryphantoidea, and Wandesioidea. Having both the setal pairs of the anal segment reduced is an autapomorphy expressed by the larvae of the Hydrachnoidea, and having one pair of anal setae re-

duced is a synapomorphy shared by larvae of Hydrovolzioidea, Eylaoidea, Piersigioidea, and Limnocharoidea.

The following autapomorphies separate Hygrobatoidea (s.T.) from the Hydryphantoidea and all other superfamilies:

Larval behavior. The apotypic behavior of the larvae is locating prospective hosts underwater. This is derived from the plesiotypical behavior "locating the host from the water surface or adjacent vegetation" (Smith & Oliver 1986), as it is expressed by Hydryphantoidea and most other Hydrachnellae. It is assumed that Acherontacaridae (Hydrovolzioidea) and Hydrachnoidea have convergently developed the apotypic behavior to locate their host underwater. They differ in this behavior from the Hygrobatoidea as they are not able to locate prospective hosts, locating the host instead in the instar in which it is used for engorgement.

Some populations and species in different taxa have lost the ability to parasitize a host. However, reduction of the parasitic life phase is interpreted as a dead end in the evolution of water mites (B.P. Smith 1988), as it is only found in isolated species or populations and never in larger clades.

Attacking Chironomidae is interpreted as plesiotypic behavior shared by Hygrobatoidea and certain Hydryphantoidea. This interpretation is based on the fact that in Hydryphantoidea a wide spectrum of hosts, including Chironomidae, is attacked, whereas in Hygrobatoidea (s.T.) Chironomidae are by far the dominant host taxon and only few taxa select other Diptera (e.g., Deuterophlebiidae), Trichoptera, or Odonata (review by Smith & Oliver 1986).

Larval morphology. According to the cladogram shown above, character states of larval morphology have to be interpreted as follows:

Autapomorphic character states in the larvae of the Hygrobatoidea (s.T.) are the reduction of the median eye and the development of paired claws on the leg tarsi. The combination of four pairs of propodosomal setae and 1-2 mediohysterosomal setae on the dorsal plate, but Lh1 (= humeral seta) not fused to the DS separates Hygrobatoidea (s.T.) from Hydrachnoidea (in the latter Lh1 is fused to the DS).

The reduction of the empodium on the terminal segment of the legs in the larval stage is an apomorphic feature convergently developed in Hygrobatoidea (s.T.) and Hydrachnoidea.

The legs of the larvae being 5-segmented is an apomorphic feature convergently developed in Hygrobatoidea (s.T.), Hydrachnoidea, and Hydrovolzioidea.

Note on adult genital field morphology. The plesiomorphic condition of the genital field is the possession of three pairs of acetabula borne in the integument near the gonopore. It is often found in taxa closely related to the Hydrachnellae as well as in subgroups of the Hydryphantoidea. Again, several of the so called "modern" water mites (Lebertioidea sensu Cook 1974) show this plesiomorphic character state, while others superfamilies suspected to be "primitive" possess acetabula apotypically situated in other parts of the body (e.g., on the coxae in the integument or on the postgenitale).

Diagnosis of the Hygrobatoidea (s.T.)

Superfamily Hygrobatoidea Koch, 1842 (s.T.):

Diagnosis.

Larva. Somatic chaetom of larvae with "2-2-2-4-4-4-4-4-2-4-4" setae per segment from anterior to posterior (segmentation concept according to Tuzovski 1987, cf. Chapter 4). Larvae fully adapted to aquatic life, searching preadult stage of host underwater and engorging and parasitizing on the emerging "aerial" adult stage. Larvae parasitize Diptera, Trichoptera, and Odonata (Exception: one species of *Arrenurus* was observed parasitizing on larvae of Coleoptera). Median eye reduced. Legs with five movable segments (basifemur and telofemur fused), and dorsal plate bearing four pairs of propodosomal setae and at most two pairs of mediohysterosomal setae.

Nymphs and Adults. Somatic chaetom of nymphs and adults with "2-2-4-4-6-4-4-4-2-4-0" setae per body segment from anterior to posterior (segmentation concept s.T.). Coxoglandulare 2 (= Cg2 = Hv) present. Chelicerae two-segmented. Palp five-segmented; palpal tibia without dorsodistal process. Hypostome without sucking disk. Acetabula present in the genital field. Median eye reduced.

Nymphal acetabula either separated and flaps rudimentary (plesiomorphic), or grouped together and surrounded by two half-ring-like homologs of the genital flaps, or these homologs fused to a complete ring (apomorphic character state found only in Hygrobatoidea s.T.), or fused with flaps to form one or two plates (convergently developed in Hydryphantoidea and Hygrobatoidea s.T.).

Adult acetabula either below movable flaps (plesiomorphic character state), or on movable genital flaps, or on plates or free in the gonopore. Body, legs and organization of genital field in adults often with sexual dimorphism.

5. SYSTEMATICS IN THE HYGROBATOIDEA KOCH, 1842 (*SENSU* TUZOVSKI 1987)

Thirty-five families are included in the Hygrobatoidea (s.T.). The taxonomic investigations in this study refer solely to "anisitsiellid-like" water mites. Hence only those taxa are redefined below that exhibit direct relationships to the Anisitsiellidae.

Following the ideas of Welbourn (1991), Smith & Cook (1991) and others, larval characters are taken as more conservative than adult characters. Therefore the changes in higher systematics suggested are based on a reassessment of larval characters. Additionally, the organization type of the provisory genital field of the deutonymphal stage is used as a key character for the systematics in the Hygrobatoidea (s.T.).

Misleading, but of major importance in former systematics, were the adult-characters "extent of secondary sclerotization of the idiosoma" and "position of acetabula in the genital field of adults." Approaches based on these characters led to contradictions in the taxonomic system (e.g., allocating the two sexes of single species of *Rheolimnesia* and *Siboneyacarus* to two different superfamilies).

Three family groups are suggested in order to separate families which are more closely related to the Anisitsiellidae-Limnesiidae complex from those only distantly related. The new family groups are named the "*Sperchon*-like," the "*Limnesia*-like," and the "*Hygrobates*-like and *Mideopsis*-like" Hygrobatoidea (s.T.). They reflect evolutionary trends. However, as there is still not enough information available on larvae and nymphs to undertake a consistent cladistic analysis, the family groups should not be raised to the rank of superfamilies. The characters separating the family groups are discussed below.

As the analysis is restricted to "anisitsiellid-like" taxa, several families of the "*Sperchon*-like," and all 24 families of "*Hygrobates*-like and *Mideopsis*-like" Hygrobatoidea (s.T.) are not treated.

The family Anisitsiellidae is split into several parts (see Table 11), with 26 genera being shifted to the family Limnesiidae and allocated to the subfamily Anisitsiellinae stat. nov. and to two new subfamilies. Three genera are placed in the Bandakiopsiidae fam. nov.

Family group "*Sperchon*-like" Hygrobatoidea

Diagnosis. Diagnostic for the family group is the combination of two characters: (a) the organization of the provisory genital field of the nymphal stage, with homologs of the genital flaps obviously present but acetabula not fused to these homologs of the genital flaps, and (b) presence of movable genital flaps in the adults. The nymphal acetabula are either separated and homologs of the genital flaps, small or grouped together and surrounded by two half-ring-like homologs of the genital flaps, or these homologs are fused to a complete ring. In some cases a secondary sclerotization starts from the outer edge of the ring, which forms a ventral plate. The acetabula are never fused to a common sclerite or to other sclerites flanking the provisory genital field. The ring-like basalsclerites of individual acetabula are never enlarged or fused to other sclerites.

Discussion. The "*Sperchon*-like" Hygrobatoidea include the six families Sperchontidae, Rutripalpidae, Oxidae, Teutoniidae, Bandakiopsiidae fam. nov., and Lebertiidae.

The main diagnostic character of the group, the organization of the genital region of the nymphal stage, shows a transformation series which is useful for taxonomic purposes. The character state is expressed in the nymphs of *Sperchonopsis*, with the acetabula separated and flaps rudimentary (as in some Hydryphantoidea). This is the plesiomorphic character state commonly found in Hydryphantoidea. The apotypical character state, found in all other genera, is with the acetabula grouped together and surrounded by two half-ring-like homologs of the genital flaps, or with these homologs fused to a complete ring. In some genera, e.g., *Oregonacarus*, a secondary sclerotization starts from this complete ring, and forms a ventral plate (see Fig. 23). Other transformation series are found in the larval stages, where for example the coxal plates are small and all separate (a plesiomorphic character state) in some species of the Sperchontidae, increased in size in other members of the same family, and show increasing degrees of fusion in the families Bandakiopsidae, Rutripalpidae, Teutoniidae, Oxidae, and Lebertiidae respectively.

Compared with the Hydryphantoidea, the half-ring- or ring-like homologs of the genital flaps surrounding the grouped acetabula in the nymphal provisory genital field are a synapomorphic character state of the "*Sperchon*-like" Hygrobatoidea (except *Sperchonopsis*). This interpretation puts *Sperchonopsis* into an position between Hydryphantoidea and Hygroba-

TABLE 11. Suggested system for the families of the Hygrobatoidea (s.T.). The position of the discussed taxa in the systems of Cook (1974), Tuzovski (1987) and in the suggested system is shown. Families Anisitsiellidae, Limnesiidae, Bandakiopsiidae fam. nov., and the three subfamilies newly adopted to the Limnesiidae are given in bold letters.

after Cook (1974)	after Tuzovski (1987)	suggested system (this study)
LEBERTOIDEA	HYGROBATOIDEA	HYGROBATOIDEA
Sperchontidae	Sperchontidae	"*Sperchon*-like" HYGROBATOIDEA
Teutoniidae	Teutoniidae	Sperchontidae
Rutripalpidae	Rutripalpidae	Rutripalpidae
Anisitsiellidae	**Anisitsiellidae**	**Bandakiopsidae fam. nov.**
Torrenticolidae	Torrenticolidae	Teutoniidae
Oxidae	Oxidae	Oxidae
Lebertiidae	Lebertiidae	Lebertiidae
	Limnesiidae	"*Limnesia*-like" HYGROBATOIDEA
HYGROBATOIDEA	Omartacaridae	Torrenticolidae
Pontarachnidae	Hygrobatidae	**Limnesiidae**
Limnesiidae	Ferradasidae	**Bandakiinae subfam. nov.**
Omartacaridae	Unionicolidae	**Bharatoniinae subfam. nov.**
Hygrobatidae	Feltriidae	**Anisitsiellinae stat. nov.**
Ferradasidae	Pionidae	"*Hygrobates* & *Mideopsis*-like"
		HYGROBATOIDEA
Unionicolidae	Astacocrotonidae	Omartacaridae
Feltriidae	Aturidae	Hygrobatidae
Pionidae	Mideidae	Ferradasidae
Astacocrotonidae	Gretacaridae	Unionicolidae
Aturidae	Momoniidae	Feltriidae
	Mideopsidae	Pionidae
ARRENUROIDEA	Uchidastygacaridae	Astacocrotonidae
Mideidae	Kantacaridae	Aturidae
Gretacaridae	Nipponacaridae	Mideidae
Momoniidae	Horreolanidae	Gretacaridae
Mideopsidae	Bogatidae	Momoniidae
Uchidastygacaridae	Chappuisididae	Mideopsidae
Kantacaridae	Krendowskiidae	Uchidastygacaridae
Nipponacaridae	Acalyptonotidae	Kantacaridae
Horreolanidae	Athienemanniidae	Nipponacaridae
Bogatidae	Harpagopalpidae	Horreolanidae
Chappuisididae	Hungarohydracaridae	Bogatidae
Krendowskiidae	Arrenuridae	Chappuisididae
Acalyptonotidae		Krendowskiidae
Athienemanniidae	PONTARACHNOIDEA	Acalyptonotidae
Harpagopalpidae	Pontarachnidae	Athienemanniidae
Hungarohydracaridae		Harpagopalpidae
Arrenuridae		Hungarohydracaridae
		Arrenuridae
		PONTARACHNOIDEA
		Pontarachnidae

toidea (s.T.), sharing the type of arrangement of the acetabula in the genital field with some taxa of the Hydryphantoidea and for example the 5-segmented legs of the larva with the latter.

Compared with "*Limnesia*-like" and „*Hygrobates*-like and *Mideopsis*-like" Hygrobatoidea, it is a symplesiomorphic character state of the "*Sperchon*-like" nymphs that the acetabula are separated and not fused to the homologs of the genital flaps.

Further information on the family Bandakiopsiidae (fam. nov.) is provided below. As none of the other families (Sperchontidae, Rutripalpidae, Teutoniidae, Oxidae, Lebertiidae) is altered in its constitution, family descriptions and keys, as given for them by Cook (1974), Smith (1982), Smith & Cook (1991) and others, remain valid.
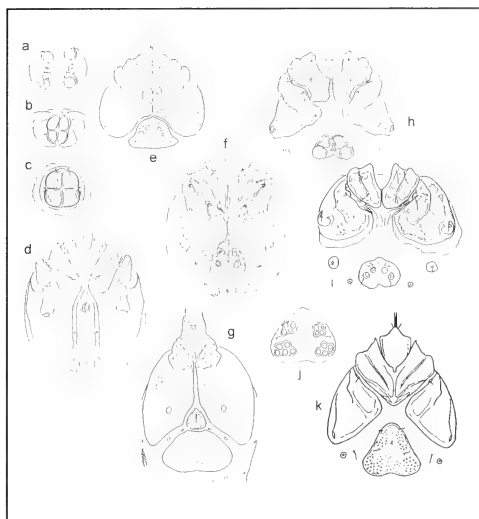

FIG. 23. The nymphal provisory genital region in "anisitsiellid-like" Hydrachnellae. Members of Hydrphantoidea (HYP), "*Sperchon*-like" Hygrobatoidea (SLH) and "*Limnesia*-like" Hygrobatoidea (LLH): (a) *Thyas pachystoma* (HYP), (b) *Oxus magnellus* (SHL), (c) *Notosperchonopsis ischiotricha* (SLH), (d) *Oregonacarus rivolicolus* (SLH), (e) *Utaxatax* sp. (LLH), (f) *Bandakia* sp. (LLH), (g) *Psammotorrenticola gracilis* (LLH), (h) *Nilotonia emarginata* (LLH), (i) *Nilotonia tegulata* (LLH), (j) *Sigthoria nilotica* (LLH), (k) *Rheolimnesia tronchoni* (LLH) [Figs. a, b from Tuzovski (1990), Fig. c from Cook (1980), Fig. d Smith (1989), Figs. e, g Gerecke (1994), Figs. f, h original, Fig. i Gerecke (1991), Fig. j Harvey (1990), Fig. k Lundblad (1953)].

Bandakiopsiidae fam. nov.

Type: *Bandakiopsis fonticola* Smith, 1979.

Diagnosis of adults. Characters of the "*Sperchon*-like" Hygrobatoidea. Complete dorsal and ventral shields present; dorsal shield bearing postocular setae and either 3 or 6 pairs of glandularia; lateral eyes are located with preocular setae and a pair of glandularia on anterolateral platelets; these platelets separated from ventral shield in three species and fused to it in one species; ventral shield bearing 4 or 5 pairs of glandularia; dorsal furrow narrow, bearing 4 pairs of slit organs and either no or 3 glandularia; coxal plates III widely separated; coxal plates IV posteriorly either slightly convex, nearly transverse and obliterate, or fused without visible suture to the ventral shield. Insertions of leg IV located at level of genital field, with well-developed condyles; genital field with slight sexual dimorphism: in males three pairs of elongated acetabula with equal distance between each other, in females distance between first and second pair slightly or clearly enlarged; legs without "swimming" setae; IV-L-6 with well-developed claws with ventral blade and bladelet or clawlet; palps with P5 long and with well-developed claws, P2 either with blunt seta in ventrolateral position (Fig. 27) or with medium strong seta in ventrodistal position; Cg4 located at the end of a finger-like sclerotization (Fig. 28), this sclerotization either short and restricted to anteromedially region of fourth coxae or elongated with Cg4 lying on anterolateral edges of first coxae or elongated, with Cg4 lying on anterolateral edges of third coxae.

Diagnosis of nymphs. Nymph with characters of the "*Sperchon*-like" Hygrobatoidea such as acetabula of provisional genital field being grouped together and homologs of genital flaps forming a tightly fitting ring around the acetabula. A secondary sclerotization arising from this ring forms an elongated ventral plate.

Venter covered by a secondary sclerotization around the excretory pore plate by the elongated plate arising from the provisory genital field and by the coxal plates. First coxal plates fused laterally to second coxal plates and ventrally to each other, a secondary sclerotization arises from the medioposterior border of the first coxae as given in Fig. 29; third coxae medially widely separated and fused to fourth coxae; fourth coxae enlarged posteriorly; furrow between elongated secondary sclerotization around genital field and medial borders of third and fourth coxae narrow.

Dorsum covered by a large anterior and a smaller posterior plate, with three platelets and two pairs of

glandularia filling the space between these two plates (Fig. 29). Lateral eyes located with preocular setae and a pair of glandularia on anterolateral platelets which are separated from ventral shield.

The deutonymph of only a single species (*Oregonacarus rivulicolus*) is known (see Smith 1989).

Diagnosis of larva. Characters of the Hygrobatoidea as given above. Coxae all free; seta R2 relatively posterior in position and drastically enlarged; Dh1 and Dh3 fused to the dorsal shield; basal segments of chelicerae free; seta sC3 present (reduced in some species of *Limnesia*, in all *Manotonia*, *Anisitsiella*, and in some Sperchontidae). Setae Vh1 and Vh2 fused to third coxa (a situation which is also found in the Rutripalpidae and Lebertiidae, and which differs clearly from the pattern expressed in *Limnesia*, *Manotonia*, and *Anisitsiella* where sclerites of seta Vh1 are fused medially to each other).

Only the larval stage of a single species (*Bandakiopsis fonticola*) is known. For a detailed description of the larvae see Smith (1982). Larvae of *Bandakiopsis fonticola* were found parasitizing the abdominal region of imagos of Dixidae (*Dixa*).

Discussion. The genera *Bandakiopsis* Smith, 1979, *Cookacarus* Barr, 1977, and *Oregonacarus* Smith, 1989 are assigned to this family. All three genera, with one species each, were reported from springs and seepage areas in a small location in extreme western North America. A new species of *Bandakiopsis* from the Himalayas is described below.

Adult, nymphal and larval characters indicate that the group is an early derivate lineage of the Hygrobatoidea (s. T.). The nymph of Bandakiopsiidae shows the provisory genital field typical of the "Sperchon-like" Hygrobatoidea. The two pairs of acetabula are surrounded by a complete ring, as in *Limnolegeria* or *Notosperchonopsis*, but equipped with a larger secondary sclerotization in Bandakiopsiidae (*Oregonacarus*). Adults show plesiomorph character states (1) in the claws at P5 being well developed, (2) in possessing condyles at the insertions of the fourth legs, (3) in the form of the coxae, resembling the coxae of *Sperchon*, *Notosperchonopsis* or Rutripalpidae (well visible in *Bandakiopsis* and *Cookacarus*, and slightly altered in *Oregonacarus* due to the finger-like protruding sclerification "carrying" the Cg4 at its tip).

The form of the adult coxae, shared by Bandakiopsiidae as well as *Sperchon*, *Notosperchonopsis* and *Rutripalpus*, fits well to some larval characters that indicate a closer relationship between these taxa, such as the (plesiomorphic) presence of normal-sized setae

Ex1 and Ex2 (reduced in all other members of the Anisitsiellidae-Limnesiidae complex). The larvae share with the larvae of Rutripalpidae (described by Gerecke & Tuzovski 2000) the shape of ventral and dorsal shields, the form and extent of fusion of the coxae (with coxae all close to each other but unfused), and the palpal tibia equipped with two claws. They differ from the larvae of Rutripalpidae in that in the latter, setae Dh1, Dh3 are free in the dorsal furrow and Vh2 is fused to the third coxae.

The shape of the adult chelicerae is very characteristic for the two species of *Bandakiopsis* (Fig. 25). Its shape is unique and differs clearly from all known chelicerae of species placed formerly under the Anisitsiellidae. However, until the chelicerae of *Oregonacarus* and *Cookacarus* are described, it remains open if this character could underline the close relationship of the three genera. A hexagonal structure is visible in the chitinized surface of *Bandakiopsis* and *Cookacarus*, especially in the palpal segments, but Smith (1989) does not describe the surface structure of *Oregonacarus*. Again it remains open if this character could underline the close relationship of all the three genera.

A synapomorphic character state of the adults shared by all members of the group is the presence of a complete ventral shield with the third coxae medially widely separated and with strongly developed condyles at the posterolateral corners of the fourth coxae.

It is impossible to draw conclusions for the whole family from the other life stages, as larval and nymphal stages are only known for one species each. Hence, the discovery and description of the as yet unknown nymphs and larvae of the Bandakiopsiidae is awaited to prove if the three genera taken out of the Anisitsiellidae represent a natural group.

Genus: *Bandakiopsis* Smith, 1979 [2 spp.]

Typus generis: *Bandakiopsis fonticola* Smith, 1979. Material examined: *Bandakiopsis fonticola* paratype, Präp. 7093, SMF; *Bandakiopsis phaluti* sp. nov.; type series, ARP. Location of genotype: holotype in CNC, type No. 15837; 1 paratype in SMF

Definition (adults)

Characters of the Bandakiopsiidae as defined above and:

- Cg4 situated at the anterolateral tip of finger-like indentation or separate platelet, which is found posterior to the suture C3/C4 in the anteromedial corner of C4 (Fig. 25).
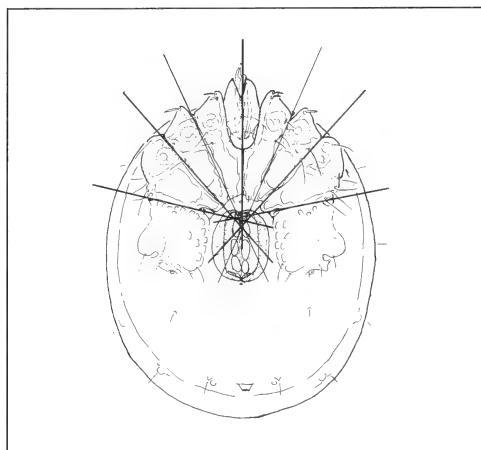
FIG. 24. "Bandakiopsis-like" organization of coxae. Note: The sutures between the coxae (indicated by straight lines) all point to a common center.

- Coxal organization "*Bandakiopsis*-like": with sutures between coxae pointing to a center in the anterior half of the genital field (Fig. 24).
- C4 nearly rectangular in shape, with well-developed condyles.
- IV-L-6 always with well-developed claws with ventral blade and clawlet.
- Chelicerae with an uninterrupted and clearly concave ventral border leading to a "banana-like" shape (Fig. 25).

Species included

Bandakiopsis fonticola Smith, 1979 was described in both sexes from seepage areas in western North America (British Columbia, Canada). The larva of this species is described by Smith (1982). A new, quite similar species *Bandakiopsis phaluti* sp. nov. (described below) was discovered in a seepage area at mount Phalut in the south-eastern Himalayas (Darjeeling, India).

Inventory (adults)

DS/VS. VS and DS complete. DS with postocular setae and 6 pairs of glandularia; dorsal furrow without glandularia and with 4 pairs of slit organs.
Eyes. Lenses on platelets anterior to the VS.
Coxae. See definition.
Cg4. See definition. Shape slightly different in males and females and between species.

GF. C4 closely impending GF. Insertions of IV-L at level of GF. Sexual dimorphism: Relative length of GF greater in females.
Ac. 3 pairs of Ac in two rows. Sexual dimorphism: In adult females the distance between the first and the second pair of acetabula reaches half the length of an acetabulum, while the third pair follows the second pair without a gap. In males all pairs of acetabula follow each other closely.
I-L-6. With several small ventral setae and a long dorsodistal hair. Always with well-developed claws with ventral blade and clawlet.
IV-L-6. Similar to I-L-6, but claw with less-developed ventral blade.
Palpus. Palpus anisitsiellid-like with a chitinization with well visible hexagonal structure; P5 long, P4 with prominent ventral hooks, P2 with "ventral" seta short, thick, blunt and shifted to a more lateral position.
Chelicerae. Total length 200–220 µm; length of claw 63–67 µm; anterior height of basal segment 40–46 µm. The characteristic shape of the chelicerae (see following fig.) is unique among all taxa which were placed under Anisitsiellidae untill now, as well as among all other members of the "*Sperchon*-like" Hygrobatoidea (s.T.).
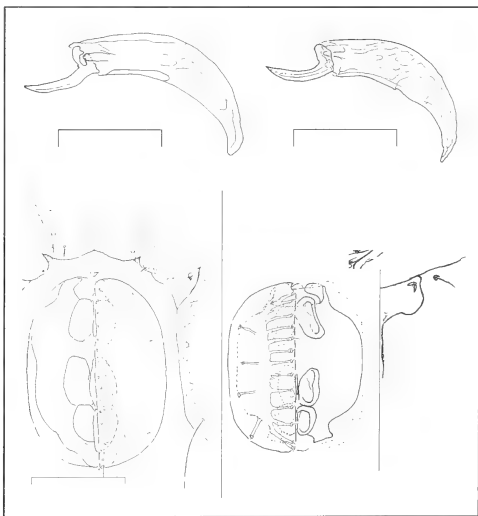

FIG. 25. *Bandakiopsis*. Shape of chelicera and Cg4. Top: chelicerae. Top left: *B. phaluti* sp. nov.. Top right: *B. fonticola*. Bottom: genital field and cg4 in females. Bottom left: *B. phaluti* sp. nov.. Bottom right: *B. fonticola*. Scale bars = 100 µm.

Further remarks

Nymph. Nymph not known. Information on a nymph of *B. fonticola* collected by Ian Smith will be published soon (pers. comm.).

Larva. Described by Smith (1982) with characters as discussed under the family description.

Habitat. Mosses and detritus in springs and seepage areas.

Distribution. The genus shows an amphi pacific distribution, with one species known from the northern Rocky Mountains (Canada) and one from the eastern Himalayas (India).

Bandakiopsis phaluti sp. nov.

Holotype: 1 male adult from coll. 1993-05-31_2 [1200 m trek from mount Phalut towards Gorki in the south-eastern Himalayas near the peak of Mount Phalut (Darjeeling, India).] Paratypes: 3 females with same data as holotype. Location: Type material in the NMB. A paratype will be deposited in the ZSI (India).

Description of male. Characters as given in generic definition, Fig. 26, and inventory. For all measurements see Table 12. Length-to-height ratio of palpal segments is P1 = 0.7, P4 = 2.1, and P5 = 3.5. Distance from posterior border of GF to posterior border of body = 270 μm. Only a single male was discovered.

Description of female. Similar to the male, except (1) distance between first and second pair of acetabula

FIG. 27. *Bandakiopsis phaluti* sp. nov. (female), Palpus. Top: medial view. Bottom: P4-P5 lateral view. Scale bars = 100 μm.

slightly enlarged, (2) gonopore relatively longer in female, and (3) female in general slightly larger than male (Table 12 and Fig. 25, 27).

Differential character. Bandakiopsis phaluti sp. nov. differs from *Bandakiopsis fonticola* Smith, 1979 mainly (1) in that the antero lateral edge of C2 is sharply pointed in the latter and rounded in *B. phaluti*, (2) a seta is present on the anterolateral edge of *B. phaluti* and absent in *B. fonticola*, (3) ventral tubercles on P4 are more prominent in *B. phaluti*, and (4) the palpal segments P4 and P5 are more elongated in *B. fonticola*, with length-to-height ratio for P4 below 2.1 in *B. phaluti* and above 2.6 in *B. fonticola*. (Respective values for P5 are 3.5 versus 3.8).

Nymphs and larva. unknown.

Habitat. All specimens were collected from silt and detritus in a seepage area near a first order stream in a small bamboo forest in the south-eastern Himalayas at 3450 m a.s.l.

Distribution. The species is known only from the type locality in Darjeeling state (India).

Derivatio nominis. Reference to the locus typicus – Mount Phalut (Darjeeling, India).

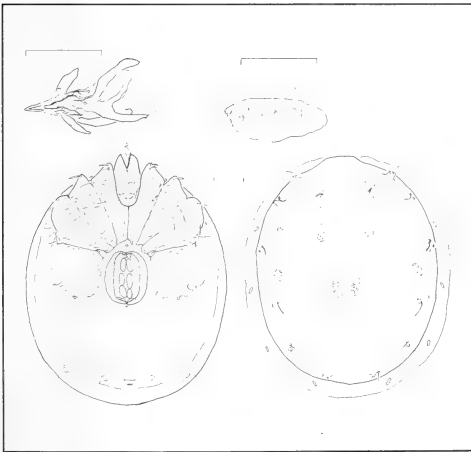FIG. 26. *Bandakiopsis phaluti* sp. nov. (male). Top left: genital sclerite of male. Top right: eye plate of female. Bottom: ventral and dorsal shield female. Scale bars = 100 μm.

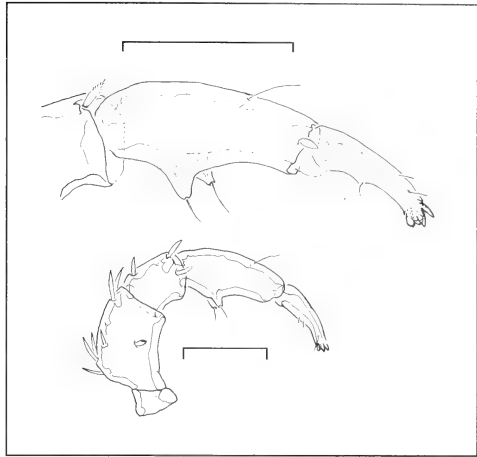### Genus: Cookacarus Barr, 1977 [1 sp.]

Typus generis: *Cookacarus columbiensis* Barr, 1977. Location of genotype: Department of Entom. and Invertebrate Zoology, Royal Ontario Museum (holotype); paratypes in CNC. No material examined

TABLE 12. *Bandakiopsis* 1: adult; [measurements in µm]; l./w. ratio = length to width ratio.

| *Bandakiopsis* Body part measurement	♂ (H)	*B. phaluti* sp. nov. Type series ♀ 0	♀ 1	♀ 2	*B. fontinalis* Smith, 1979 from Smith 1979 ♂ 3	5 ♀	new data* 1 ♀*
Dorsum							
length	742	835	870	880	730-782	838-902	851
width	600	790	730	700	?	?	706
Dorsal shield							
length	740	810	824	726	718-770	784-842	822
width	585	616	650	630	568-614	630-680	661
Eye platelets							
length	-	135	–	–	?	?	134
Coxae							
length suture C1/C1	135	135	145	143	?	?	120
left to right width C3 /C3	513	550	550	530	?	?	540
left to right distance Cg4	196	220	224	196	?	?	245
Genital field							
GF to end of body	270	314	333	336	?	?	360
genital opening: width	121	138	141	134	130-146	160-176	150
genital opening: length	154	202	195	190	148-158	202-218	199
gen. opening: l./w. ratio	1.27	1.46	1.38	1.41	?	?	1.33
genital flaps: length	156	202	213	190	?	?	190
Gnathosoma							
ventral length	150	-	133	-	?	?	–
Chelicera							
claw: length	63	-	67	-	?	?	67
basal segm.: length	150	161	161	-	?	?	150
basal segm.: ant. height	40	42	46	-	?	?	42
Palpal segments							
P1							
length/height	35/50	35/48	35/48	-	27-33/?	29-37/?	23/50
length/height ratio	0.70	0.73	0.73	-	?	?	0.46
% of total length	8.5 %	7.7 %	7.8 %	-	?	?	5.6 %
P2							
length/height	109/63	120/76	120/72	-	104-110/?	113-123/?	104/64
length/height ratio	1.73	1.58	1.67	-	?	?	1.63
% of total length	26.5 %	26.4 %	26.6 %	-	?	?	25.2 %
P3							
length/height	70/51	76/63	70/60	-	59-63/?	68-73/?	66/47
length/height ratio	1.37	1.21	1.17	-	?	?	1.40
% of total length	12.4 %	16.7 %	15.5 %	-	?	?	16.2 %
P4							
length/height	130/63	133/70	133/67	-	119-127/?	134-140/?	138/52
length/height ratio	2.06	1.90	1.99	-	?	?	2.65
% of total length	31.6 %	29.2 %	29.5 %	-	?	?	33.50 %
P5							
length/height	87/25	91/27	93/28	-	74-79/?	77-85/?	81/21
length/height ratio	3.48	3.37	3.32	-	?	?	3.86
% of total length	21.1 %	20.0 %	20.6 %	-	?	?	19.66 %
Palpus: total length	412	455	451	-	388	440	412
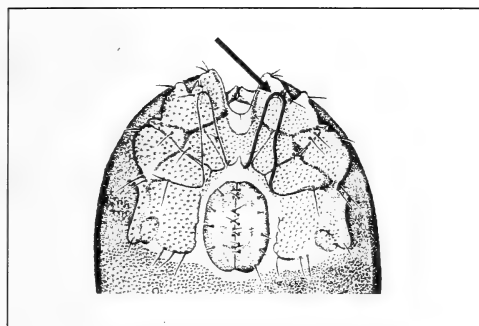
FIG. 28. *Cookacarus columbiensis* Ventral view, showing coxal organization. The coxoglandulare 4 (Cg4) are found at the tips of finger-like protrusions. Shape of left protrusion indicated by a thick line; position of left Cg4 indicated by an arrow [Fig. from Barr (1977), modified].

Definition (adults)

Characters of the Bandakiopsiidae as defined above and:

- Coxal organization "*Bandakiopsis*-like" (see under G. *Bandakiopsis*).
- VS complete.
- Cg4 placed at anterolateral edges of C1, situated at the tip of sclerotized finger-like protrusion arising from the region medial to the suture C3/C4.

Species included

Cookacarus columbiensis Barr, 1977, described with females only, is the only known species of the genus.

Inventory (adults)

DS/VS. VS and DS complete. DS with postocular setae (R2) and 6 pairs of glandularia; dorsal furrow without glandularia and with 4 pairs of slit organs.
Eyes. Lenses on platelets anterior to the VS.
Coxae. See definition.
Cg4. See definition.
GF. C4 closely impending GF. Insertions of IV-L at level of GF.
Ac. Three pairs of Ac in two rows. In adult females the distance between the first and second pair of acetabula about equal to the length of the second acetabulum; the third pair follows the second pair without a gap.
I-L-6. With several small hairs and a few setae ventrally; with a long dorsodistal hair and with well-developed claws with ventral blade and clawlet.

IV-L-6. Similar to I-L-6, but claw with less-developed ventral blade.
Palpus. Palpus with a chitinization with well visible hexagonal structure; P5 with long claws; no prominent ventral hooks on P4, "ventral" seta on P2 slightly shorter than ventral length of P2, and shifted to a more lateral position.
Chelicerae. Not described.

Further remarks

Males and nymphs. I. Smith (pers. comm.) collected males and nymphs of the species and will publish descriptions soon.
Larva. Not known
Habitat. Mosses and detritus in springs and seepage areas.
Distribution. As yet only described from the type locality in western North America (British Columbia, Canada).

Genus: *Oregonacarus* Smith, 1989 [1 sp.]

Typus generis: *Oregonacarus rivolicolus* Smith, 1989. Location of types: Holotype: Male adult; slide No. 20270, CNC; Paratypes: ROM. Specimens deposited in SMF are most probably lost. No material examined

Definition (adults)

Characters of the Bandakiopsiidae as defined above and:

- Coxal organization "*Bandakiopsis*-like" (see under G. *Bandakiopsis*), but anterior to the genital field with C3 protruding medially.
- VS complete.
- Cg4 placed at anterolateral edges of C3, situated at the tip of sclerotized finger-like protrusion arising from the suture C3/C4 (arrow in Fig. 29).

Species included

Oregonacarus rivolicolus Smith, 1989 described with males, females and nymphs is the only known species of the genus.

Inventory (adults)

DS/VS. VS and DS complete. DS bearing postocular setae and three pairs of glandularia laterally; dorsal furrow bearing three pairs of glandularia and 4 pairs of slit organs; ventral shield with three pairs of glandularia marginally and one pair flanking the excretory pore.
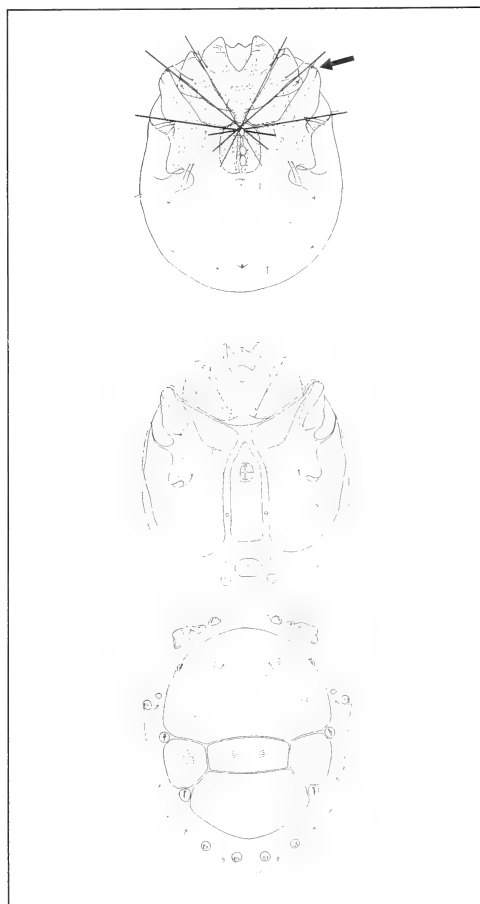*Eyes.* Lenses on platelets anterior to the VS.

FIG. 29. *Oregonacarus rivolicolus* Top: Ventral view (female). The coxoglandulare 4 (Cg4) are found at the tips of finger-like protrusions. Position of left Cg4 indicated by an arrow. Bottom: Ventral and dorsal view of nymph [Figs. from Smith (1989), partly modified].

Coxae. Coxae nearly rectangular in shape, with well-developed condyles and with posterior border obliterate.

Cg4. See definition.

GF. C4 closely impending GF. Insertions of IV-L at level of GF.

Ac. Three pairs of Ac in two rows. Sexual dimorphism: In adult females the distance between the first and the second pair of acetabula about equal to the length of the second acetabulum; the third pair follows the second pair without a gap. In males the acetabula pairs follow each other without a gap.

I-L-6. With several small hairs in the distal half; without long dorsodistal hair as in *Bandakiopsis* and *Cookacarus*, but with a small seta in an identical position and with well-developed claws with ventral blade and clawlet.

IV-L-6. Similar to I-L-6 (fide text in Smith 1989).

Palpus. Palpus very similar in shape and chaetotaxy to the palpus of Cookacarus; P5 with long claws; no prominent ventral hooks on P4, "ventral" seta on P2 slightly shorter than ventral length of P2, and shifted to a more lateral position.

Chelicerae. Not described.

Further remarks

Nymph. Nymph similar to adults but less sclerotized, with DS and VS as given in Fig. 29 and with provisory genital field typical of the "*Sperchon*-like" Hygrobatoidea (s.T.): 2 pairs of acetabula grouped very closely together and homologs of genital flaps fused to a complete ring closely surrounding the acetabula; a longitudinal secondary sclerotization is fused to this ring and separated on each side by a small furrow from C3 and C4 (for a detailed description, see Smith 1989).

Larva. Not known.

Habitat. Mosses and detritus in springs and seepage areas and rocky riffles in small cascading streams.

Distribution. Western North America (Oregon, California).

Family group "*Limnesia*-like" Hygrobatoidea

Diagnosis. Diagnostic for the family group is the combination of two characters: (a) In the nymphal stage the acetabula are always fused to the homologs of the genital flaps into a usually triangular plate, while (b) in the adult stage well-developed movable genital flaps are present at least in the female. In the adult stage the acetabula may be situated either free below movable genital flaps, or fused to the movable genital flaps, or (in males) these flaps may be fused to each other to form a plate.

Discussion. The "*Limnesia*-like" Hygrobatoidea include two families, the Torrenticolidae and the Limnesiidae. Most of the genera earlier assigned to the Anisitsiellidae are placed by me within the Limnesiidae.

The arrangement of the acetabula in the genital field shows an interesting transformation series. In adults, the plesiomorphic condition is found in the family Torrenticolidae and the subfamily Bandakiinae

(subfam. nov. in Limnesiidae), where three pairs of acetabula lie in two medial rows under movable genital flaps, and the basal ring sclerites of the individual acetabula are not enlarged – a character state symplesiomorph with "*Sperchon*-like" Hygrobatoidea. In the subfamily Anisitsiellinae, (subfam. stat. nov. in Limnesiidae) the basal ring sclerites are thin in most of the species. However, especially in the subgenus *Dartia*, enlarged basal sclerites are common, and in some species either the posterior two or all three are fused to form a pair of parallel sclerites which carry the acetabula. While the fused basal sclerites of the acetabula lie completely below the movable genital flaps in *Dartia*, they are adpressed to the outer medial margin of the genital flaps in *Shivatonia* gen. nov., and are only partly covered by the genital flaps in *Bharatonia* (both placed in Bharatoniinae, subfam. nov. in Limnesiidae). In the female of *Meramecia diamphida* (Neomamersinae), the basal sclerites of the acetabula are fully fused (without suture) to the medial margin of the genital flaps. The series of hairs indicating the former medial margin of the genital flaps is still situated lateral to the acetabula in this species. In other species, e.g., in *Meramecia* and typically in the genus *Limnesia*, the acetabula are incorporated into the flaps, sometimes quite lateral in position. The series of hairs indicating the medial margin of the genital flaps in *Meramecia*, is not present in *Limnesia*, because some of the setae are shifted medially and are bordering the "new" medial margin of the movable genital flaps (formed by the enlarged basal sclerites of the acetabula). In males, e.g., in the Limnesiinae, the flaps may be fused anteriorly and/or posteriorly, forming an immovable genital plate, which is the most derived character state of this transformation sequence.

Family Limnesiidae

Limnesiidae Thor, 1900. Nyt Mag. Naturv. 38:3
Anisitsiellidae Koenike, 1910 [syn. nov.]

Diagnosis for adults. Characters of the "*Limnesia*-like" Hygrobatoidea. Acetabula either lying below movable genital flaps or lying on movable genital flaps in females (and males of some subfamilies, but these flaps fused forming immovable acetabula carrying plates in the males of many species).

Palp five-segmented; P2 with single ventral seta; this seta is either thin or peg-like and either sessile or located on a tubercle of variable length. (98% of the adults posses this seta. However, it is reduced in some species (1) with a retrusible gnathosoma, (2) in the strongly modified palps of some interstitial forms, and (3) in few species of *Mixolimnesia* with an otherwise "typical" palp.).

Cg4 (in this group often named "Glandula Limnesiae") is either present medial to bifurcation of suture lines between third and fourth coxae, or appearing to lie on the third or second coxae, or these glands lacking.

Sclerotization varying from weak, with no dorsalia or ventralia, to well-developed dorsal and ventral shields in some species; coxae in four groups or exhibiting varying degrees of fusion; fourth coxae tending to be somewhat triangular in shape in many species.

Fourth legs either with or without claws; swimming hairs present or absent.

Diagnosis of nymphs. Characters of the „*Limnesia*-like" Hygrobatoidea. Basal sclerites of the acetabula in the provisory genital field fused to the homologs of the genital flaps forming a medial platelet (lacking a gonopore); this plate with two pairs of acetabula in those species with three pairs in the adults, but more than two pairs may be present in the nymphs of polyacetabulate species. Seta on ventral surface of P2 typical of the adults is missing in the nymphal stages of most species.

Diagnosis of larva. Dorsal plate large, covering most of the idiosoma in length, and either narrow and clearly not covering entire width of dorsum and pointed posteriorly (in all Limnesiinae), or narrow to broad, clearly elongated, maximum width anterior to midpoint – sometimes just posterior to the outer pair of eyes – and oval posteriorly (in all Anisitsiellinae and Tyrrelliinae), or nearly circular (in Bandakiinae).

Length of dorsal plate is larger in Limnesiinae (230–320 µm) than in the other subfamilies (180–220 µm).

Porosity of sclerotization either rather continuous (*Nilotonia* (*Manotonia*) *tegulata*, Anisitsiellinae), or in regular groups finely punctate and hexagonally reticulate (in *Nilotonia* (*Dartiella*) *longipora*, *Anisitsiella costenus*, Anisitsiellinae and Bandakiinae), or dorsal plate provided anteriorly with striae (most species of Limnesiinae).

Dorsal shield with four pairs of propodosomal setae, A1, R1, A2 and R2; first three pairs all very close to the anterolateral margin of the dorsal shield, with seta A2 always located at level between inner and outer pairs of eyes. Seta R2 located close to LP2 either at same level medially to PL (in Bandakiinae), or lat-

TABLE 13. Limnesiidae, larvae: variation in distances between anterior and posterior eye lenses and in length of DS.

	1 distance between eyes	2 length of dorsal shield	3 ratio: distance 1 to length 2	4 ratio: length 2 to distance 1
Nilotonia (*Manotonia*) *tegulata*	16	205	12.8	0.078
Nilotonia longipora	16	210	13.1	0.076
Anisitsiellides costenus	18	230	12.8	0.078
Limnesia min. (of 12 spec.)	16	235	14.7	0.068
Limnesia max. (of 12 spec.)	25	320	12.8	0.078
Tyrrellia noodti	25	190	7.6	0.132
Bandakia phreatica	35	200	5.7	0.175
Utaxatax newelli	40	180	4.5	0.222

eral, posterolateral or exactly posterior to PL (in Anisitsiellinae and Limnesiinae).

Setae R2 generally present, but in Tyrrelliinae possibly small or reduced to insertions (Viets (1953a) mentions only three anterior pairs for the dorsal plate of *Tyrrellia crenophila*; Besch (1962) depicts in a rough sketch only three propodosomal setae on the dorsal plate of *T. noodti*).

Humeral setae either borne on lateral extensions of C2 and C3 (6 spp. of *Limnesia*) or in dorsal furrow (5 spp. of *Limnesia*, 2 spp. of Anisitsiellinae, 3 spp. of Bandakiinae).

Two pairs of lateral eyes on platelets. Platelets either separate, or adpressed to each other (*Utaxatax newelli*), or fused. Distance (in µm) between inner and outer pair of lenses (center to center) as given in the following table (measurements in µm):

Dorsal furrow either bearing 7 pairs of setae (other than humeral setae), including 4 pairs of mediohysterosomal setae (= Mh1-Mh4) and three pairs of laterohysterosomal setae (= Lh1-Lh3), or dorsal furrow with 4 pairs of setae (with setae Mh1, Lh1, Lh2 and Lh3 reduced to alveoli in Anisitsiellinae).

Venter with C1-C3 on each side separate (*Utaxatax*, Bandakiinae) or variously fused, with suture lines between plates incomplete at least medially. C1 with seta Cs1 posteromedially and Cs2 anterolaterally; C2 with or without seta Cs3 (present only in Bandakiinae); C3 usually without posterior projections (in one species, *Bandakia phreatica*, with slight posterior projections), C3 bearing setae Cs4 anteriorly (in Bandakiinae, Anisitsiellinae and Tyrrelliinae) or more posteriorly (in Limnesiinae).

Seta Cs3 is reduced in Tyrrelliinae (known larval stage of one species, fide Besch 1962), Anisitsiellinae (known larval stages of 3 species in two genera), Limnesiinae (this feature is well described in the larval stages of 12 species of *Limnesia*). It is also reduced in some species belonging to Sperchontidae (*Sperchonopsis*). However, it is present in all other known Hygrobatoidea (s.T.) larvae.

One or two pairs of urstigmata. The larvae of *Tyrrellia* and of some species of *Limnesia* possess two pairs of urstigmata. However, out of the 11 species of *Limnesia* in which this character is adequately described (Wainstein 1966, 1980; Prasad & Cook 1972, Wainstein & Tuzovski 1974; Tuzovski 1990, 1997), 6 species possess only one pair of urstigmata and 5 possess two pairs. The presence of only one pair of urstigmata is the plesiomorphic character state, expressed in Anisitsiellinae, Bandakiinae, and most other water mites.

Excretory pore plate variously shaped; from little larger than excretory pore (Tyrrelliinae, Anisitsiellinae, Limnesiinae) to occupying entire region posteromedial to coxal plates (some Bandakiinae). Excretory pore plate bearing two pairs of setae Ex1 and Ex2, or, in one species (*Bandakia phreatica*, Bandakiinae), three pairs of setae, including V2 at posterolateral angles. Setae Ex1 and Ex2 reduced to alveoli or reduced to short fine hairs. Setae V1 or V2 never fused to coxal plates. Setae V1 reduced to alveoli or small hairs in all Limnesiidae and situated on a medial chordate platelet in Anisitsiellinae.

Basal segments of chelicerae varying from slender to thick, and always medially separate from one

another. Pedipalps with tibial claws undivided or bifurcate; tarsi short and button-like bearing 6 to 7 setae and one solenidium; tarsal setae always shorter than pedipalp.

Solenidia on legs very short and thin. The importance and usefulness of leg chaetotaxy and solenidiotaxy has been stressed by various authors, including Smith & Cook (1991) and Wainstein (1980). However, different systems are in use for counting the various types of setae present on the legs of water mite larva, which makes it difficult to compare the results. The main difference is that Smith, Cook and co-workers do not distinguish between eupathidia and setae, but between solenidia and "other setae," while Wainstein, Tuzovski and co-workers do not distinguish solenidia and setae but separate eupathidia from "other setae."

Discussion. The family Limnesiidae is defined here, in a broad sense, as an assemblage of all clades in which the fusion of the basal sclerites of the acetabula with the movable genital flaps is expressed in a transformation series in the adult stages, while the equivalent process is already completed in the nymphal stage. Limnesiidae understood in this sense contains the genera and subfamilies assigned to them by Cook (1974), some other more recently discovered taxa, and three subfamilies (Bandakiinae, Bharatoniinae and Anisitsiellinae) assigned to them in this study. These three subfamilies contain most of the genera which were placed under the Anisitsiellidae earlier. Limnesiidae in this broad sense includes 12 subfamilies, more than 50 genera, and around 500 species.

The character state of the basal segments of the chelicerae being separate in the larval stages of all Limnesiidae is taken as a symplesiomorphy. They are fused in Torrenticolidae and many „Hygrobates-like and *Mideopsis*-like" Hygrobatoidea and separate or only partly are fused in all "*Sperchon*-like" Hygrobatoidea.

Seta C3 being reduced in the larval stages is a synapomorphy of Anisitsiellinae, Tyrrelliinae and Limnesiinae, convergently developed in some species of the Sperchontidae. Seta C3 is present in all other known larval stages of the Hygrobatoidea (s.T.) and in Bandakiinae, underlining that the latter are still only tentatively assigned to the group (see below).

Two preliminary autapomorphies of the Anisitsiellinae, (including approx. 90 species, of which there are 3 with known larval stages), are the character states (1) "larval setae Vh1 both fused to a common chordate medial platelet" and (2) "larval setae Dh1, Lh2, Lh3 and Lh4 reduced to alveoli"; in all other Limne-

siidae these setae are present, and in all other Hygrobatoidea (s.T.) setae V1 are free or fused to the coxal plates III or to the excretory pore plate.

Two preliminary autapomorphies of the Limnesiinae (approx. 250 species, 12 with known larval stages) are the character states (1) "position of larval setae C4" – these are located in Limnesiinae clearly posterior to the remnants of the suture between C2 and C3, but are located directly on the remnants of this suture (and at a clearly more anterior level of the ventral shield) in all other Limnesiidae, and (2) "larval dorsal shield pointed posteriorly"; in all other Limnesiidae the posterior outline of the dorsal shield is oval or roundish.

The tarsus of larval palp being short and button-like with 6 or 7 short setae is a character state shared by all Limnesiidae and is also found in Torrenticolidae, Rutripalpidae, Bandakiopsiidae and – with thickened setae – in Oxidae. It separates the Limnesiidae from the Sperchontidae, Teutoniidae, and Lebertiidae which possess one or more strongly elongated setae on this segment.

Although it is easy to define a character set diagnostic for the Limnesiidae (e.g., characters of the "*Limnesia*-like" Hygrobatoidea and seta V1 not fused to C3 in the larval stage), there is still neither in the larval nor in the nymphal or adult stages a known synapomorphy of this diverse family. Larvae are adequately described for not more than 20 species, representing 7 genera and 4 subfamilies. Further descriptions of larvae are definitely needed to obtain a more appropriate picture of the family and to decide if the Limnesiidae, or any subgroup thereof, is holophyletic. The revision of the genera formerly placed under the Anisitsiellidae presented in this study must be followed by revisions of as yet untreated subfamilies of the Limnesiidae (A revision on Protolimnesiinae is currently beiing undertaken by T. Goldschmidt).

Subfamily Bandakiinae (subfam. nov.)

Bandakia Thor, 1913. Zool. Anz. 43: 40. Type: *Bandakia concreta* Thor. Monobasic.
Drammenia Thor, 1913. Zool.Anz. 43: 40. Type: *Drammenia elongata* Thor. Monobasic.

Diagnosis for adults. Characters of the family Limnesiidae. Complete dorsal shield present. Ventral shield complete, but with suture lines extending laterally from region of second coxae and separating off a pair of anterior eye-bearing sclerites in many species. Dorsal furrow narrow. Insertion of fourth legs situated in posterolateral (*Bandakia*) or anterolateral (*Utaxatax*)

position on fourth coxae; insertions of IV-L circular or with condyles.

Genital field, in both sexes, with three pairs of elongated acetabula, situated in the soft integument next to the gonopore below movable genital flaps. Third pair of acetabula sometimes less elongated than anterior two pairs. Basal sclerites of acetabula not enlarged.

Coxal organization with Cg4 together with medial part of C4 shifted anteriorly and covers medial part of C3 (cf. Fig. 23). Cg4 situated at anterolateral corner of the protruding part of C4. In the adults of most species an additional transverse suture separates this anterior part of C4 (which covers C3) from the remaining surface of this plate. As a result, C3 seems to be divided into a medial platelet and a larger lateral portion. In these cases Cg4 is found at the anterolateral corner of the platelet medial from C3.

Palp five-segmented and varying from "mamersopsid-like" to "anisitsiellid-like", always with a small peg-like seta at the distal end of P5.

Chelicerae of typical shape and always with a strongly pointed dorsal elevation in the middle of the basal segment (Fig. 30).

Legs stocky; swimming hairs absent; fourth legs terminating in well-developed claws.

Diagnosis of nymphs. Characters of the family Limnesiidae. Basal sclerites of the two pairs of acetabula fused with homologs of the genital flaps forming a triangular plate in the provisory genital field; the plate is of varying size from twice the length of the acetabula pairs to clearly enlarged (Fig. 23).

Ventral shield absent. Fourth coxae usually enlarged by lateral and posterior secondary sclerotizations and always with medial part of the fourth coxae projecting anteriorly, overlapping the medial part of the third coxae. Cg4 situated in the anterolateral edge of this projection (Fig. 23). Dorsum without complete dorsal shield, but either with two larger plates with anterior plate larger than posterior plate (*Bandakia*) or with a single central plate (*Utaxatax*).

The seta on ventral surface of P2, typical of the adults, is absent in nymphs. Other characters similar to adults.

Characteristics of larva. See "Characteristics of larva" and "Discussion" under family Limnesiidae.

Discussion. Bandakiinae include the two genera *Bandakia* and *Utaxatax*, which are well defined as holophyletic according to autapomorphies in the adult stages, and which seem to be only distantly related to the other subfamilies of the Limnesiidae due to clear

differences in the larval stage. They belong clearly to the "*Limnesia*-like" Hygrobatoidea, on the basis of character combinations in the adult and nymphal genital region.

Genus: *Bandakia* Thor, 1913 [20 spp.]

Typus generis (T.g.): *Bandakia concreta* Thor, 1913 Location of T.g.: Type material lost. Material examined: *Bandakia concreta*, Präp. 4068, SMF; Präp. CRG. *Bandakia corsica*, CRG. *Bandakia curvipalpis* sp. nov. *Bandakia gangetica* sp. nov. *Bandakia himachali* sp. nov. *Bandakia norma* holotype, CRG. *Bandakia orientalis* holotype Präp. 4490, SMF. *Bandakia speciosa* "type" Präp. 7637, SMF.

Definition (adults)

Characters of the Bandakiinae as defined above and:
• Insertion of IV-L not displaced anteriorly (as in genus *Utaxatax*).

Species included

A list including distributional data on the accepted species, the species-groups, and information on subspecies and synonymies is given below. The list contains the new species from the Himalayas, though further species from North America will be published soon by Smith & Cook (pers. comm.).

Inventory

DS/VS. VS and DS complete.

Eyes. Eye-region organized in three types: (1) Lenses free in dorsal furrow. (2) Lenses on platelets. (3) Lenses fused into anterolateral edges of the VS.

Coxae. See definition. The shape of the posterior border of C4 and the angles between sutures C3/C4 and C2/C3 are helpful in distinguishing several species.

Cg4. See definition. The feature "Cg4 at anterolateral edge of a platelet separated medially from C3" is also found in *Utaxatax* and two other species of "*Limnesia*-like" Hygrobatoidea (*M. mesoamericana* and *Gilatonia triscutata*).

GF. C4 closely impending GF completely in *B. mexicana* and *B. wendyae*, anterior two-thirds in *B. orientalis* and *B. corsica*, anterior half in *B. hoffmannae*. In all other species the posteromedial edge of C4 is rounded and C4 does not closely impend GF. Insertions of IV-L at level of GF – varying from anterior to posterior end of GF.

Ac. Three pairs in row; in most species gaps between first, second and third acetabula pair of equal size or (as in most species) without gaps; third pair of Ac rarely smaller and more circular.

TABLE 14. List of species groups, species and synonyms in *Bandakia*.

Genus *Bandakia*	Author	Distribution
B. anisitspalpis group		
Bandakia anisitsipalpis	Cook, 1963	N. America (N. Carolina)
Bandakia curvipalpis	sp. nov.	Himalaya, India (Darjeeling)
Bandakia fragilis	Smith, 1979	N. America (Oregon)
Bandakia gangetica	sp. nov.	Himalaya, India (Garhwal)
Bandakia himachali	sp. nov.	Himalaya, India (H.P.)
Bandakia japonica	Immamura, 1965	Asia, Japan
Bandakia kulluensis	sp. nov.	Himalaya, India (H.P.)
Bandakia oregonensis	Smith, 1979	N. America (Oregon)
B. longipalpis group		
Bandakia hoffmannae	Cramer & Smith, 1991	C. America, Mexico
Bandakia longipalpis	Cook, 1974	N. America
B. vietsi group		
Bandakia bieberi	Bader, 1994	Europe (Switzerland); syn. of *concreta*?
Bandakia borealis	Smith, 1979	N. America
Bandakia concreta	Thor, 1913	Europe
B. concreta longissima	Schwoerbel, 1955	Europe
Bandakia corsica	Angelier, 1951	Europe, Corsica (France)
Bandakia norma	Gerecke, 1990	Europe, Sicily (Italy)
Bandakia orientalis	Viets, 1935	Asia, Java (Indonesia)
Bandakia phreatica	Cook, 1974	N. America
Bandakia similes	Cook, 1963	N. America
Bandakia speciosa	Viets, 1953	Europe
Bandakia vietsi	Cook, 1961	N. America, Michigan
B. incertae sedis		
Bandakia mexicana	Cramer & Smith, 1991	Mexico, C. America
Bandakia wendyae	Wiles, 1991	Asia, Malaysia
Invalid names		Synonyms / Remarks
B. concreta bremensis	(Viets, 1920)	syn of *B. concreta*
B. concreta hercynia	(Viets, 1925)	syn of *B. concreta*
B. crassipalpis	(Thor, 1913)	syn of *B. concreta*
B. elongata	(Thor, 1913)	syn of *B. concreta*
B. elongata	Cook, 1963	nom. praeocc.: new name = *B. longipalpis*
B. hercynia	(Viets, 1925)	comp. *B. concreta hercynia* = syn. of *B. concreta*

I-L-6. I-L-6 often with hairs; claw with ventral blade, ventral clawlet and dorsal hair-like clawlet.

IV-L-6. IV-L-6 with about four terminal setae of which a medial one is about as long as the claw. Claw hook-like, sometimes with fine medial clawlet.

Palpus. "Anisitsiellid-like" or "mamersopsid-like."

Chelicerae. Basal segment of chelicerae approx. mid-dorsally always with strongly pointed elevation.

Nymphs and larvae

Adequate descriptions of larvae of *B. borealis* and *B. vietsi* were given by Smith (1979), and of *B. phreatica* by Smith (1982). The relevance of larval characters for systematics is treated under Limnesiidae in sections "Characteristics of larva" and "Discussion", and in the discussion of the taxonomic placement of the genus given below.

Nymphs are known from *B. concreta* (e.g., Viets 1920), *B. speciosa* (treated as *B. corsica* in Schwoerbel 1961), *B. longipalpis* (Cook 1963), and *B. himachali* sp. nov.

Taxonomical placement of the genus

The first species described (*B. concreta* Thor ,1913) showed a mamersopsid palp and was therefore assigned as a new taxon in the Mamersopsidae. When Cook (1963) found a *Bandakia* with an "anisitsiellid-like" palp (*B. anisitsipalpis*), he suggested reducing the Mamersopsidae to subfamily rank and placing them within the Anisitsiellidae.

In the current study I place *Bandakia* under the "*Limnesia*-like" Hygrobatoidea (s.T.), because of certain larval characters (see above) and because of the acetabula being fused to the homologs of the genital flaps in their nymphal stages. They are placed in the Limnesiidae because of the possession of a seta on the ventral surface of P2. The organization of the dorsal shield and the coxae separates them from the Torrenticolidae. They are placed in a separate subfamily Bandakiinae (subfam. nov.) because characters of the larvae clearly separate them from members of the Anisitsiellinae (stat. nov.), as well as from Limnesiinae and from all known larvae of the "*Sperchon*-like" Hygrobatoidea (s.T.).

Key to species groups and selected species

1 Coxa C2 forming a common suture C2/C2 medially . . . . *B. mexicana*
1* not so 2
2 Palpus "mamersopsid-like"; eyes fused into ventral shield . . . . *vietsi*-group
2* not so 3
3 Palpus "anisitsiellid-like", but with short segments and without ventral seta on P2 . . . . *B. wendyae*
3* Palpus "anisitsiellid-like"; eyes either free or on platelets or fused into ventral shield 4
4 P4 with ventral tubercles; eyes either free or on platelets; claws at I-L-6 usually with blade and clawlets . . . . *anisitsipalpis*-group
4* P4 without ventral tubercles; eyes fused into ventral shield; claws at I-L-6 usually hook-like with dorsal and/or ventral clawlet . . . . . . *longipalpis*-group

Discussion of species groups and untypical species

The genus was divided into three groups by Smith (1979): the *anisitsipalpis*-group, the *longipalpis*-group, and the *vietsi*-group.

Gerecke (1990) retained the *anisitsipalpis*- and the *vietsi*-group only, selecting the fusion of the eye-plates with the ventral shield as the only relevant character.

Even if species groups are without phylogenetic value, they do separate groups of more homogeneous species from each other and are retained for taxonomical reasons. The revision of the genus allows the following groupings:

Vietsi-group [8 spp.]

The *vietsi*-group harbors all species of the genus *Bandakia* with a "mamersopsid-like" palpus and with eyes fused into the anterolateral edges of the ventral shield.

In the *vietsi*-group all species except *B. orientalis* are quite similar in appearance. However, *B. orientalis* differs from the other species (1) in the organization of the coxae, with the C2 nearly touching each other medially while they are clearly separated by the first coxae in the other species of the group, and (2) the claws with blades and a ventral clawlet at IV-L-6 (all other species of the group possess hook-like claws with or without small clawlets at IV-L-6), according to Bader (1994).

The species included in the *vietsi*-group here are: *B. borealis*, *B. bieberi*, *B. concreta*, *B. corsica*, *B. norma*, *B. orientalis*, *B. phreatica*, *B. similis*, *B. speciosa* and *B. vietsi*.

Longipalpis-group [2 spp.]

The *longipalpis*-group includes the two species (1) with an "anisitsiellid-like" palp, (2) without ventral tubercles on P4, and (3) with lenses included in the anterolateral edges of ventral shield.

The group consists of two species, which can be easily separated: In *B. hoffmannae* Cramer & Smith, 1991, the suture C1/C1 is clearly longer than the distance between genital field and posterior end of the suture C1/C1. In *B. longipalpis* Cook, 1963, the suture C1/C1 is shorter or about as long as the distance between genital field and posterior end of the suture C1/C1.

Anisitsipalpis-group [6 spp.]

The *anisitsipalpis*-group harbors all species with (1) an "anisitsiellid-like" palp, (2) with ventral hooks on P4, and (3) with eyes situated on platelets (which may be fused medially) or situated free in the integument.

Further characters are (4) acetabula large and contiguous, occupying nearly entire length of gonopore medially, (5) dorsal furrow with 4 or 2 pairs of glan-

dularia, (6) ventral shield with 1 or three pairs of glandularia, (7), insertions of IV-L with or without condyles.

B. japonica Imamura, 1965 differs in that the eye lenses are not situated on platelets, but free in the soft integument of the dorsal furrow. Imamura (1965) does mention this in the text and shows it in his drawings.

The *anisitsipalpis*-group unites 8 species with a quite similar morphology regarding coxal organization or shape and chaetotaxy of the palpus. However, the species can be distinguished by the combination of the following characters: (1) number of glandularia in the dorsal furrow, (2) shape of the posterior border of the dorsal shield, (3) the presence, size and shape of the platelets carrying the eye-lenses, (4) presence or absence of condyles at insertions of IV-L, (5) the form of the protruding part of C4 carrying Cg4 on

FIG. 31. *Bandakia himachali* sp. nov.: Leg 4 to leg 1 (from top to bottom). Scale bar = 100 µm.
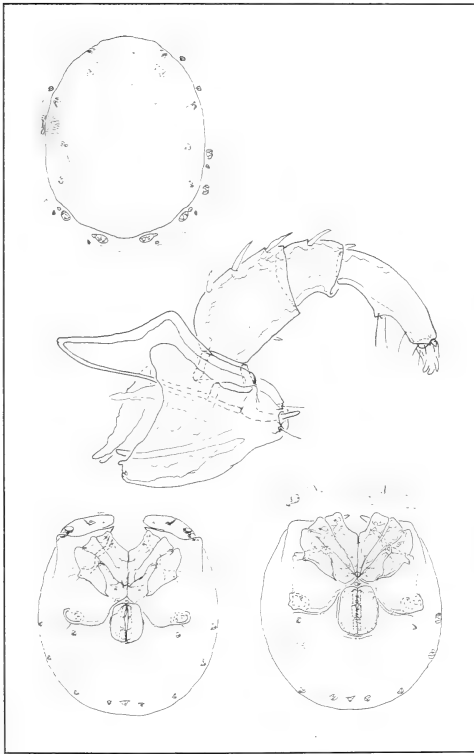

FIG. 30. *Bandakia himachali* sp. nov.: Dorsal plate of male (top), gnathosoma, palpus and chelicera (middle), ventral shield with eye plates of male (bottom left) and female (bottom right).
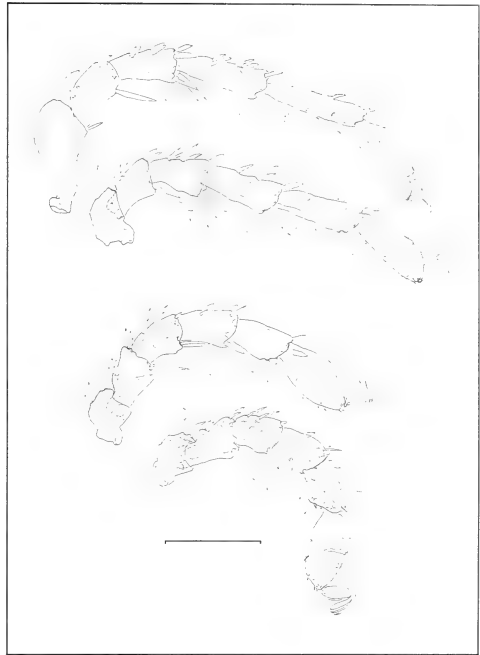
its lateral edge, (6) the length/height ratio of the palpal segments, (7) the shape of posterior suture of C4 and (8) the angle between sutures C4/C3 and C3/C2.

The species included into the *anisitsipalpis*-group here are: *B. anisitsipalpis*, *B. curvipalpis* (sp. nov.), *B. fragilis*, *B. himachali* (sp. nov.), *B. japonica*, *B. kulluensis* (spec. noc.), *B. gangetica* (sp. nov.) and *B. oregonensis*.

All new species from the Himalayas (described below) belong to this group.

Bandakia himachali sp. nov.

Holotype: 1 male adult from collection "1995-07-6[95/122]" (Karol-Nala, Kullu Valley, Himachal Pradesh, India). Paratypes: 1 male and 1 female (adults) from collection "1995-07-13 [95/170]" (Kunoi-Nala, Kullu Valley, Himachal Pradesh, India); 1 female adult from collection "1996-06-16 [96/247]" (Naggar-Nala, Kullu Valley, Himachal Pradesh, India).
Type material placed in the NMB. A parataype will be deposited in the ZSI (India).

Description of male. As shown in Fig. 30 and with characters of the *anisitsipalpis*-group. Dorsal shield with length 540–593 µm and width 390–405 µm.
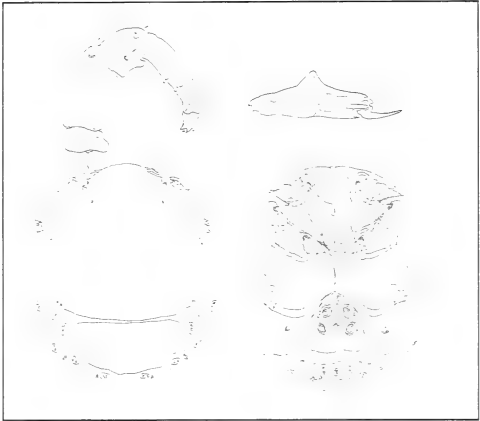
FIG. 32. *Bandakia himachali* sp. nov. (nymphal stage): Palpus (top left), chelicerae (top right), dorsal view (bottom left), ventral view (bottom right).

All measurements for the different specimens are given in Table 15 and Table 16. With 4 pairs of glandularia in the dorsal furrow. Cg2 on lateral border between C2 and C3, forming the end of the suture C2/C3. Cg4 found at the tip of a finger-like protrusion on suture C2/C3 in the lateral part of C3. Posterior border of DS slightly retreating near the two posterior pairs of glandularia. Insertions of IV-L with strongly developed condyles. Eye-platelets with lenses, glandularium and a hair-like seta each. The two platelets are medially nearly adpressed, with parts of their medial border parallel. Dark pigments below eye-lenses present. Genital opening with Length-to-height ratio between 1.1 and 1.2. Palpus with Length-to-height ratio of P2 of 1.6-1.7 and with ratio of length P2 to length P4 of 1.9-1.1. Legs shown in Fig. 31, with I-L-6 broad and excavation for claws large starting from about mid-length in the dorsal side.

Description of female. Similar to male.

TABLE 15. *Bandakia* 1: Idiosoma data *B. himachali* sp. nov. and *B. curvipalpis* sp. nov. [measurements in μm].

Bandakia	*B. curvipalpis* sp. nov.					*B. himachali* sp. nov.			
Collection	7/93	7/93	7/93	7/93	14/93	95/247	95/170	95/170	95/122
No. on slide	2	4	1	3			2	1	
sex [m=male; f=female]	m	m ?	f	f ?	f ?	f	f	m	m (H)
Dorsal shield: length	525	525	495	530	504	585	540	593	540
Dorsal shield: width	405	392	390	430	378	420	425	405	390
DS: length/width ratio	1.3	1.3	1.3	1.2	1.3	1.4	1.3	1.5	1.4
Eye platelets									
median distance	fused	fused	fused	fused	fused	4.6	2.5	2	4.1
length	150	-	140	-	-	155	160	160	155
Coxae									
dist.: gnathos. – GF	125	120	127	127	123	146	144	144	144
length suture C1/C1	75	70	-	75	63	98	103	100	100
left - right width C3	290	275	290	293	275	312	295	320	293
left - right distance Cg4	125	122	130	130	130	157	172	161	148
paramed. sut. C3: length	70	66	63	69	63	90	92	93	92
post. margins: GF/C4	-80	-95	-87	-92	-82	-70	-63	-62	-42
Genital field (GF)									
GF to end of body	225	220	185	225	172	227	215	210	199
genital opening: width	110	110	100	105	96	115	114	118	95
genital opening: length	155	160	150	160	155	140	125	140	107
gen. opening: l./w. ratio	1.4	1.5	1.5	1.5	1.6	1.2	1.1	1.2	1.1
genital flaps: length	155	155	150	155	150	138	138	136	117
Chelicera									
basal segm.: length.	-	120	-	129	120	132	137	132	120
claw: length	-	45	-	46	41	46	43	42	37
basal segm.: max. height	-	48	-	48	48	52	52	51	54
basal segm.: ant. height	-	30	-	-	-	-	-	29	-

TABLE 16. *Bandakia* 2: Palpal measurements for *Bandakia curvipalpis* sp. nov. and *B. himachali* sp. nov. [measurements in µm].

Bandakia	*B. curvipalpis* sp. nov.					*B. himachali* sp. nov.			
Collection	7/93	7/93	7/93	7/93	14/93	95/247	95/170	95/170	95/122
(spec. no. on slide)	2	4	1	3			2	1	
sex [m=male; f = fem.]	m	m ?	f	f ?	f ?	f	f	m	m (H)
Palpal segments									
P1-length	-	23	-	24	23	17	19	20	18
P1-height	-	34.5	-	36	33	46	41	40	38
P1-length/height ratio	-	0.7	-	0.7	0.7	0.4	0.5	0.5	0.5
P1: % of total length	-	6.9	-	7.0	6.6	6.3	7.8	7.5	7.2
P2-length	-	94	-	99	94	92	90	89	84
P2-height		52		55.5	57	57	54	56	52
P2-length/height ratio	-	1.8	-	1.8	1.6	1.6	1.7	1.6	1.6
P2: % of total length	-	28.2	-	28.9	26.9	34.1	34.6	33.5	33.6
P3-length	-	63	-	63	63	51	38	47	42
P3-height	-	38	-	39	39	38	38	39	37
P3-length/height ratio	-	1.7	-	1.6	1.6	1.3	1.0	1.2	1.1
P3: % of total length	-	18.9	-	18.4	18.0	18.9	18.3	17.7	16.8
P4-length	-	125	-	129	140	86	87	87	83
P4-height (incl. hook)	-	24	-	23	24	24	23	23	23
P4-length/height ratio	-	5.2	-	5.6	5.8	3.6	3.8	3.8	3.6
P4: % of total length	-	37.5	-	37.6	40.0	31.9	33.9	32.7	33.2
P5-length	-	28	-	28	30	24	23	23	23
P5-height	-	11.5	-	11.5	11.5	14	15	14	14.5
P5-length/height ratio	-	2.4	-	2.4	2.6	1.7	1.5	1.6	1.8
P5: % of total length	-	8.4	-	8.2	8.6	8.9	8.9	8.6	9.4
Palpus: total length	-	333	-	343	350	270	257	266	250
length ratio P2/P4	-	0.8	-	0.8	0.7	1.1	1.0	1.0	1.0

Nymph. Similar to adult and: Dorsally with two large plates of which anterior is largest; provisory genital field typical of "*Limnesia*-like" Hygrobatoidea (s.T.) with Ac fused to homologs of the genital flaps; medial part of C4 protruding over C3 carrying Cg4 in the anterolateral edge; P2 without ventral seta; dark pigmentation below eye-lenses present.

Larva. Unknown.

Habitat. The 4 specimens were collected in three different streams in the Kullu Valley (Himachal Pradesh, India) at an altitude of 1800–2000 m a.s.l. Three specimens were in collections from mosses and detritus and one was discovered in a driftsample taken about 200 m below a waterfall.

Distribution. Known only from the Kullu Valley (Himachal Pradesh, India) in the western Himalayas.

Derivatio nominis. Reference to the locus typicus in the state Himachal Pradesh (India).

Discussion. The species is separated from the other members of the *anisitsipalpis*-group by the combination of the following characters: (1) strongly developed condyles (as in *B. fragilis* and *B. oregonensis*), (2) 4 pairs of glandularia in the dorsal furrow (as in *B. fragilis* and *B. anisitsipalpis*) and (3) eye-platelets medially nearly adpressed with a partly medial border (as in *B. oregonensis* and in 2 of the 3 other species from the Himalayas described below). A strong and dark pigmentation below the eye-lenses is as well characteristic for this species.

Bandakia curvipalpis sp. nov.

Holotype: 1 male adult from collection "1993-05-30_1 [7/93]" (spring brook, 2,5 h trek from Sandakphu towards Sarbakum-Phalut, Darjeeling, India). Paratypes: 1 male, 2 females ?? with same data as holotype; 1 female (?) adult from collection "1993-05-31_3 [14/93]" (mountain brook in
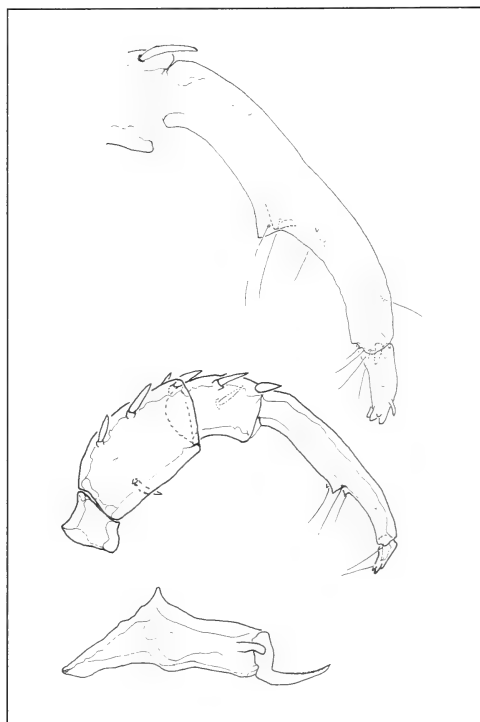
FIG. 33. *Bandakia curvipalpis* sp. nov. (male): Palpus P4-5 (top), palpus P1-5 (middle), chelicera (bottom).

bamboo forest, 1.2 km trek from Phalut towards Gorkey, Darjeeling, India). Type material in the NMB. A paratype will be deposited in the ZSI (Calcutta, India).

Description of male. With characters of the *anisitsipalpis*-group and as shown in Fig. 33. All measurements for the different specimens are given in Table 15 and Table 16. With two pairs of glandularia in the dorsal furrow. Sclerotization around these two pairs small, about twice the size of the gland. Cg4
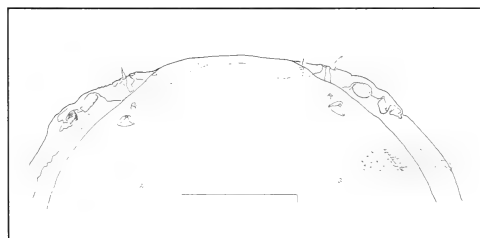
FIG. 34. *Bandakia curvipalpis* sp. nov.: Dorsal view of anterior part. Scale bar = 100 μm.

found at the tip of a finger-like protrusion on suture C2/C3. Cg4 located at about mid-length of suture C2/C3. Posterior border of DS slightly retreating near the two posterior pairs of glandularia. Insertions of IV-L with well-developed condyles. Eye-platelets fused medially and carrying lenses, a glandularium and a hair-like seta on each side. No dark pigment below eye-lenses present. Genital opening with Length-to-height ratio between 1.4 and 1.6.

Chelicerae with dorsal processus sharply pointed. Palpus with total length = 333–350 μm, with Length-to-height ratio of P2 = 1.6–1.8 and with ratio between length P2 and length P4 = 0.7–0.8. Legs with I-L-6 slender (Length-to-height ratio in I-L-6 = 3.2, compared with 2.1 in *B. himachali*). First three pairs of legs with claws with ventral blade and clawlet; claw at IV-L-6 hook-like.
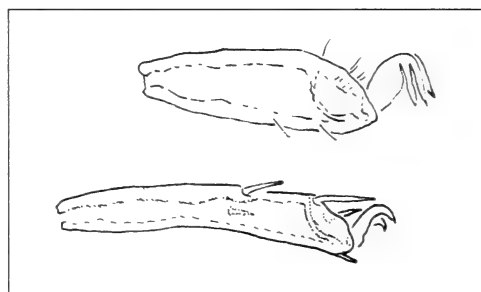

FIG. 35. *Bandakia curvipalpis* sp. nov. (female).: I-L-6 (top), IV-L-6 (bottom).

Description of female. Similar to male.
Nymphs and larva. Unknown.
Habitat. All specimens were discovered in mosses and from detritus in mountain streams at an altitude of 3450 – 3500 m a.s.l.
Distribution. Known only from the region of the type locality. The 5 specimens were collected in two different streams in Darjeeling (India).
Derivatio nominis. The name refers to the shape of the palp.
Discussion. The species is easily separated from the other members of the *anisitsipalpis*-group by the eye-plates being medially fused. It differs from the other Indian species in the total length of the palp (333–350 μm in *B. curvipalpis* versus 230–275 μm in the other Indian species) and in the slender P4 (Length-to-height ratio 5.2–5.8 versus 2.7–4.4 in the other Asian species).

TABLE 17. *Bandakia* 3: Measurements of the idiosoma of *Bandakia gangetica* sp. nov. (*B.g.*) and *Bandakia kulluensis* sp. nov. (*B.k.*) compared with other species. (*B.o.*) = *B. oregonensis*, (*B.f.*) = *B. fragilis*, (*B.j.*) = *B. japonica*.

Bandakia	*B.g.* sp. nov.	*B.k.* sp. nov.	*B.a.* Cook 1963	*B.o.* Smith, 1979	*B.o.* Smith, 1979	*B.f.* Smith, 1979	*B.j.* Ima, 1965
Collection	93/34	95/58					
(No. of specimens)	(1)	(1)	(1)	(5)	(5)	(4)	(1)
sex [m = male; f = fem.]	m?	f	f (H)	m	f	f	f (H)
Dorsal shield: length	430	522	516	580-662	658-722	466-512	-
Dorsal shield: width	293	383	365	367-452	448-494	298-328	-
DS: length/width ratio	1.5	1.4	1.4	-	-	-	-
Eye platelets							
median distance	3.5	8.1	-	-	-	-	(-)
length	139	152	-	-	-	-	
Coxae							
dist.: gnathos. – GF	111	117	-	-	-	-	-
length suture C1/C1	81	78	-	-	-	-	-
left to right width C3	235	293	-	-	-	-	-
left - right dist. Cg4	115	148	-	-	-	-	-
paramed. sut. C3: lgth	44	61	-	-	-	-	-
post. margins: GF/C4	-46	-46	-	-	-	-	-
Genital field (GF)							
GF to end of body	132	200	-	-	-	-	-
genital opening: width	83	103	104	112-122	136-152	106-122	93
genital opening: lgth.	110	128	145	124-152	178-194	148-164	120
gen. opening: l./w. rat.	1.3	1.2	1.4	-	-	-	1.29
genital flaps: length	107	135	-	-	-	-	-
Chelicera							
basal segm.: length	-	136	-	-	-	-	-
claw: length	-	46	-	-	-	-	-
bas. segm.: ht. max.	-	46	-	-	-	-	-
basal segm.: ant. hgth.	-	24	-	-	-	-	-

Bandakia gangetica sp. nov.

Holotype: 1 male (?) adult from collection "1993-06-10 [34/93]" (waterfall with mosses (carbonate-rich), 27 km after Narendar Nagar, north of Rishikesh, H.P, India) Location: Type in the NMB.

Description of male. With characters of the *anisitsi-palpis*-group and as shown in Fig.. 36. All measurements for the specimen are given in Table 17 and Table 18.

Three pairs of glandularia in the dorsal furrow, with extended secondary sclerotization around the two posterior pairs being clearly enlarged (70–75 µm in length). Cg2 at lateral border between C2 and C3, forming the end of the suture C2/C3. Cg4 located on C3, just medial from mid-length of suture C2/C3 at the tip of a finger-like protrusion. Posterior border of DS slightly retreating near the two posterior pairs of glandularia. Insertions of IV-L without condyles. Eye-platelets not fused medially, carrying lenses, a glandularium and a hair-like seta each. No dark pigment below eye-lenses present. Genital opening with Length-to-height ratio 1.3.

Chelicerae lost. Palpus with Length-to-height ratio of P2 1.7 and with length P2 versus length P4 1.1.

TABLE 18. *Bandakia* 4: Measurements of the palp of *Bandakia gangetica* sp. nov. (*B.g.*) and *Bandakia kulluensis* sp. nov. (*B.k.*) compared with literature data from other species. (*B.o.*) = *B. oregonensis*, (*B.f.*) = *B. fragilis*, (*B.j.*) = *B. japonica*.

Bandakia	*B.g.* sp. nov.	*B.k.* sp. nov.	*B.a.* Cook 1963	*B.o.* Smith, 1979	*B.o.* Smith, 1979	*B.f.* Smith, 1979	*B.j.* Ima, 1965
Collection	93/34	95/58					
(No. of specimens)	(1)	(1)	(1)	(5)	(5)	(4)	(1)
sex [m = male; f = fem.]	m?	f	f (H)	m	f	f	f (H)
Palpal segments							
P1-length	17	23	21	27-32	29-37	23-29	21
P1-height	37	50	-	-	-	-	30
P1-length/height ratio	0.5	0.5	-	-	-	-	0.7
P1: % of total length	7.2	7.8	7.7	-	-	-	7.9
P2-length	81	110	91	93-103	107-121	96-105	69
P2-height	48	70	57	-	-	-	45
P2-length/height ratio	1.7	1.6	1.6	-	-	-	1.5
P2: % of total length	33.8	37.3	33.3	-	-	-	26.0
P3-length	44	52	50	53-61	59-69	50-55	45
P3-height	34.5	50	-	-	-	-	32
P3-length/height ratio	1.3	1.0	-	-	-	-	1.4
P3: % of total length	18.6	17.6	18.3	-	-	-	17.0
P4-length	76	87	87	135-143	138-157	105-116	105
P4-height (incl. hook)	21	29	-	-	-	-	24
P4-length/height ratio	3.6	3.0	-	-	-	-	4.4
P4: % of total length	32.1	29.5	31.9	-	-	-	39.6
P5-length	18.5	23	24	29-31	29-35	23-28	25
P5-height	11.5	17	-	-	-	-	-
P5-length/height ratio	1.6	1.4	-	-	-	-	-
P5: % of total length	7.8	8.0	8.8	-	-	-	9.4
Palpus: total length	236.5	295	273	337-370	362-419	297-333	265
length ratio P2/P4	1.07	1.26	1.05	0.70	0.70	0.90	0.66

Legs with I-L-6 stocky (Length-to-height ratio in I-L-6 = 2.3). First three pairs of legs with claws with ventral blade and clawlet; claw at IV-L-6 hook-like with small ventral clawlet.

Female, Nymphs and larva. unknown.

Habitat. The specimen was discovered in collections from mosses of a carbonate-rich waterfall at an altitude of 1200 m a.s.l.

Distribution. Known only from the type locality in the Garhwal Himalayas (India).

Derivatio nominis. The name refers to the locus typicus situated near the river Ganga (India).

Discussion. The species is easily separated from the other members of the anisitsipalpis-group by the enlarged glandular plates posterior of the dorsal shield.

Bandakia kulluensis sp. nov.

Holotype: 1 female adult from collection "1993-06-10 [34/93]" (waterfall with mosses, Kunoi-Nala, Kullu-Valley, Himachal Pradesh, India). Location of type material: Type in the NMB.

Description of female. With characters of the anisitsipalpis-group and as shown in Fig. 37 and Fig. 38. All measurements for the specimen are given in Table 17 and Table 18. With four pairs of glandularia in the dorsal furrow (posterior most pair 45 μm in length). Cg2 10-15 μm medially from lateral border of C2, near the lateral end of the sutur C2/C3. Cg4 found on C3 just medial from mid-length of suture C2/C3 at the tip of a finger-like protrusion. Cg2 situated 10-15 μm medial of lateral end of suture C2/C3.
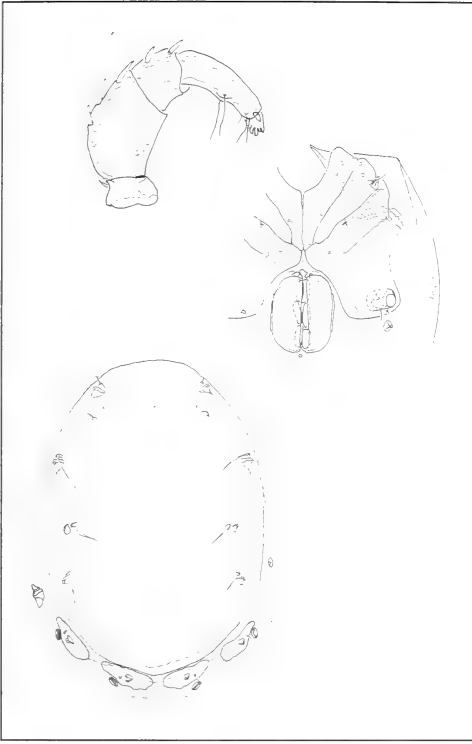
FIG. 36. *Bandakia gangetica* sp. nov. (male).: Palpus (top), ventral shield (middle), dorsal shield (bottom).

Posterior border of DS clearly retreating at level of the two posterior pairs of glandularia. Insertions of IV-L with slightly developed condyles. Eye-platelets not fused medially, carrying lenses, a glandularium and a hair-like seta each. No dark pigments below eye-lenses present. Genital opening with Length-to-height ratio 1.2.

Palpus with length-to-height ratio of P4 3.0 (P2: 1.6) and with ratio of length P2 to length P4 1.26. Legs with I-L-6 stocky (length-to-height ratio in I-L-6 = 2.4 (compared to 2.1 in *B. himachali* and 3.2 in *B. curvipalpis*). First three pairs of legs with claws with ventral blade and clawlet; claw at IV-L-6 claw hook-like.

Male, Nymphs and larva. Unknown.

Habitat. The specimen was found in collections from mosses at a waterfall at an altitude of 1800 m a.s.l.

Distribution. Known only from the type locality in the Kullu Valley (Himachal Pradesh, India) in the south-western Himalayas.

Derivatio nominis. The name refers to the locus typicus situated in the Kullu Valley (Himachal Pradesh, India).

Discussion. P4 is more stocky in *B. kulluensis* sp. nov. (length/height ratio = 3.0) than in *B. gangetica* sp. nov. and *B. himachali* sp. nov. (length/height ratio = 3.6–3.8) or in *B. curvipalpis* sp. nov. (5.2–5.8). Among the species of the *anisitsipalpis*-group, *B. kulluensis* sp. nov. is the one with the highest dorsal length ratio P2 / P4 (1.26 in *B. kulluensis* sp. nov. versus 0.70–1.07 in other species of the *anisitsipalpis*-group). *B. kulluensis* sp. nov. differs from *B. gangetica* sp. nov. in that the size of the plates posterior to the dorsal shield are not enlarged (75 µm in *B. gangetica* sp. nov. versus 45 µm in *B. kulluensis* sp. nov.). Furthermore Cg2 is situated next to the lateral border of C2, forming the
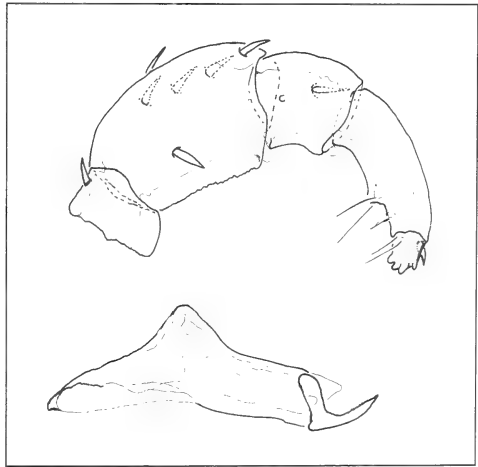
FIG. 37. *Bandakia kulluensis* sp. nov. (female). Top: palpus. Bottom: chelicera.

FIG. 38. *Bandakia kulluensis* sp. nov. (female). C4 with IV-L-1: the insertion of IV-L shows slightly projecting condyles.

lateral end of suture C2/C3 in *B. himachali* sp. nov. and *B. gangetica* sp. nov., but is situated 10–15 μm medial to this end in *B. kulluensis* sp. nov.

Taxa incertae sedis

Bandakia mexicana

The species *B. mexicana* was discovered in a spring brook in Mexico and placed into the *vietsi*-group by Cramer & Smith (1991). The taxonomic placement was based on its "mamersopsid-like" plapus, four glandularia in the dorsal furrow and eyes fused into anterolateral edges of the ventral shield. However, *B. mexicana* differs from all other species of Bandakiinae in its organizational form of the ventral shield: (1) with anterior end of genital field at level of insertions of IV-L, (2) with posteromedial edges of C4 sharply pointed – similar to the situation in *Mamersopsides* (Anisitsiellinae stat. nov.) or *Siboneyacarus* (Protolimnesiinae), and (3) with C2/C2 with medial suture line (as in some primitive Limnesiidae, e.g., *Siboneyacarus*) and not separated by C1/C1 (as in all other members of the subfamily). Furthermore, the anterior border of the dorsal shield is interrupted in a particular manner not found in any other species of the subfamily or related subfamilies.

Unfortunately information on the form of the chelicera is missing. Until the chelicerae of the adult and nymphs or larvae of the species are described, its position in the genus *Bandakia* will remain doubtful.

Bandakia wendyae

The species *B. wendyae* was collected from "allochthonous detritus in shallow slow moving water flowing over tree roots" in a rainforest brook (tributary of Sungai Gomback) in Malaysia and assigned to the genus *Bandakia* by Wiles (1991). It is similar to *B. curvipalpis* in that the eye-bearing sclerites are fused together medially. It differs in several characters from all other species of this genus and subfamily: (1) The chelicerae (as depicted in Fig. 2c, p. 44 in Wiles 1991) do not show the pointed dorsomedian processus at the basal segment, (2) the palpus is very untypically short and without a ventral seta on P2, (3) Cg4 are not found on the platelet median to C3, (4) the dorsal furrow has a single pair of glandularia only, and (5) the strong sexual dimorphism in the size of the platelet medial to C3, which is not found to a similar extent in any other member of the Bandakiinae.

Genus: *Utaxatax* Habeeb, 1964 [2 sg., 9 spp.]

Typus generis: *Utaxatax californiensis* Habeeb ,1964
Location of t.g.: ROM (?). Material examined: *Utaxatax* (s.s.) *brahmeri*, sp. nov.; *Utaxatax* (s.s.) *crassipalpis* sp. nov.; *Utaxatax* (s.s.) *gereckei* sp. nov.; *Utaxatax* (s.s.) *parvati* sp. nov.; *Utaxatax* (s.s.) *newelli*, Präp. M760191 CRG; *Utaxatax* (s.s.) *ovalis* Paratypus Präp. 6068 SMF; *Utaxatax* (*Rospatax*) *ventriplax* Holotypus CRG.

Definition (adults)

Characters of the Bandakiinae as defined above and:
• Insertion of IV-L displaced anteriorly; situated at level of insertions of III-L or anterolateral to them.

Species included

In the following are listed the accepted species (and distribution data):
(1) *Utaxatax* (s.s.) *brahmeri* sp. nov.; (Himalaya, India)
(2) *Utaxatax* (s.s.) *californiensis* Habeeb, 1964; (N. America)
(3) *Utaxatax* (s.s.) *crassipalpis* sp. nov. ; (Himalaya, India)
(4) *Utaxatax* (s.s.) *gereckei* sp. nov. ; (Himalaya, India)
(5) *Utaxatax* (s.s.) *luteus* Habeeb, 1982; (N. America)
(6) *Utaxatax* (s.s.) *newelli* (Habeeb, 1959) ; (N. America)
(7) *Utaxatax* (s.s.) *ovalis* Cook, 1974; (N. America)
(8) *Utaxatax* (s.s.) *parvati* sp. nov. ; (Himalaya, India)
(9) *Utaxatax* (*Rospatax*) *ventriplax* Gerecke, 1988; (Europe, Italy and Spain – pers comm.: R. Gerecke)

Inventory (adults)

DS/VS. VS and DS complete, DS with postocularia and 3–4 pairs of glandularia, dorsal furrow wide containing 5–6 pairs of glandularia.
Eyes. Lenses free in dorsal furrow (sg. *Rospatax*) or lenses on platelets (sg. *Utaxatax*).
Coxae. Suture C2/C3 concave, suture C3/C3 parallel and adpressed in medial part, posterior border of C4 without suture and fully fused into ventral shield in most species.
Cg4. See definition of Bandakiinae. The same feature is found in the genus *Bandakia* and two other species of early derived Hygrobatoidea (*Mamersella mesoamericana* and *Gilatonia triscutata*).
GF. Anterior border of GF posterior to level of insertions of IV-L.
Ac. Three pairs of Ac in row; no gaps between first, second and third pair.

I-L-6. I-L-6 usually with several hairs. Claws at I-L-6 hook-like with one ventral and one dorsal clawlet; if a ventral blade is present it is poorly developed only. (From I-L-6 towards IV-L-6 there is a general tendency in many genera to simplify the claws towards a hook-like form and to reduce ventral blades or clawlets).

IV-L. See definition. IV-L in some species with extremely strong setation on segments 3–5.

IV-L-6. IV-L-6 with well-developed hook-like claw (and in some species with a ventral or dorsal clawlet).

Palpus. The palpus is "anisitsiellid-like" in eight species and mamersopsid-like in one species (described below). P2 and P3 both with one seta at distoventral lateral side. These setae are more than half as long as the respective segments (or strong and thick if the palpus is "mamersopsid-like"). P4 in its distal half with two minute ventral protuberances accompanied by one long hair-like seta each.

Chelicerae. The chelicerae always show a strong and pointed median processus on the dorsal border of the basal segment.

Genital sclerit. According to Gerecke (1988), the particular type of the ejaculatory complex in *Utaxatax* could have evolved by compression of a *Bandakia*-like ejaculatory complex. It is very reduced in size and organization, and is compressed longitudinally, so that the distal arms lie near the proximal arms. All parts of the ejaculatory complex show weak sclerotization, while the knob-shaped tips of the posterior arms are somewhat more sclerotized.

Gnathosoma. Usually with a slightly convex ventral margin, a short rostrum and more or less blunt or weakly pointed processes.

Nymphs and larva

Nymph. Described by Gerecke (1994).

Larva. Described by Smith (1982).

Discussion of subgenera and species

Utaxatax (s.s.) *newelli* (Habeeb 1959) is found commonly in British Columbia (Canada) and in the northwestern USA. Habeeb named this species according to the drawings given by Newell (1959) in the second edition of "Freshwater Biology" as a new species of *Mamersella*. When he erected *Utaxatax* for *U.* (s.s.) *californiensis* Habeeb, 1964 he shifted *Mamersella newelli* to the new genus. Cook (1974) added *Utaxatax* (s.s.) *ovalis* and Habeeb (1982) *Utaxatax* (s.s.) *luteus* as the third and fourth species of the genus.

All these species were easily seperated from all other Anisitsiellidae due to the characteristic form of C4, with the insertions of IV-L displaced anteriorly into a position lateral to the insertions of III-L. The genus seemed restricted to western North America until 1988, when Gerecke erected a new subgenus *Utaxatax* (*Rospatax*) for a species (*U.* (*R.*) *ventriplax*) discovered on Sicily (Italy, Europe).

U. (*Rospatax*) differs from *Utaxatax* sensu strictu in the eye-lenses lying free in the dorsal furrow, and the anterior coxal groups fused medially (suture C1/C1) and posteriorly (suture C2/C3), while in the latter the eye-lenses are situated on platelets and the anterior coxal groups are free medially and posteriorly.

Gerecke (1988) notes a sexual dimorphism in the claws of III-L of *U.* (*Rospatax*) *ventriplax*: In the female the claw possesses a dorsal clawlet missing in the male.
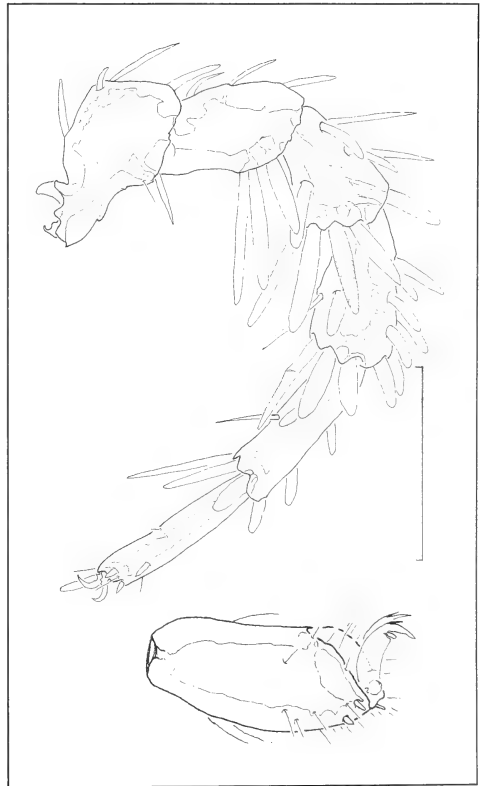

FIG. 39. *Utaxatax newelli* Top: IV-L-1-6. Bottom: II-L-6. Scale bar = 100 μm.

The investigations on water mites from the Himalayas, by the author, led to the discovery of three new species belonging to *Utaxatax* sensu strictu. Hence today this subgenus shows an amphipacific distribution, while *U. (Rospatax)* is known from Europe only.

Description of new species

Utaxatax (s.s.) *brahmeri* sp. nov.

Holotype: 1 male adult from collection "1995-05-31 [13/93]" (muddy detritus from a spring in a bamboo forest; on trek from Phalut to Gorkhey after 1200 m; Darjeeling, India). Paratypes: 3 males with same data as holotype; 1 male from collection "1993-05-30 [8/93]" mountain brook 2 h trek from Molley, on trek Sandakpuh-Sabarkum; 4 h from Sandakpuh. 1 female from collection "1995-07-10 [`95/147]" (seepage area / head waters of Kunoi-Nala, Kullu Valley, H.P., India).

Type material placed in the NMB. A parataype will be deposited in the ZSI (Calcutta, India).

Description of male. Characters as given in the definition and inventory for the subgenus *Utaxatax*. DS with postocularia and 4 pairs of glandularia; eye-lenses on platelets; palps "anisitsiellid-like"; C4 extending posterior to the GF for approx. half the length of the GF. No major differences between *U. brahmeri* and *U. ventriplax* (Gerecke 1988, Figs. 4, 5) regarding leg chaetotaxy.

Description of females. Similar to males.

Nymphs and larva. Unknown

Habitat. Discovered in a spring and two small first order streams.

Distribution. Known from Darjeeling in the eastern and Himachal Pradesh in the western Himalayas.

TABLE 19. *Utaxatax brahmeri* sp. nov. 1: Idiosoma [measurements in µm], n.d. = not dissected.

| *Utaxatax*	*U. brahmeri*	*U. brahmeri*	*U. brahmeri*	*U. brahmeri*
Collection	13/93	13/93	13/93	95/147
(Specimen number)	(3)	(1)	(2)	
sex [m = male; f = female]	m (holotype)	m	m	f
Dorsal shield (DS): length	540	535	459 455	
Dorsal shield: width	360	360	276	264
DS: length/width	1,5	1,49	1,66	1,72
No. of glandularia in DS	4	4	4	4
Postocularia: medial - lateral	m	m	m	m
median distance	n. d.	17	n. d.	n. d.
length	n. d.	105	n. d.	n. d.
Coxae				
median length C3	56	57	54	56
length suture C1/C1	46	45	40	45
left to right width C3/C3	305	295	237	246
left to right distance Cg4	90	81	52	52
paramedian suture C3: lgth.	110	105	65	78
posterior margins: GF to C4	105	102	72	78
Genital field (GF)				
GF to end of body	290	258	206	224
genital opening: width	92	88	67	78
genital opening: length	122	115	94	101
gen. opening: l./w. ratio	1,33	1,31	1,40	1,29
genital flaps: length	126	123	105	101
Chelicera				
basal segment: length	n. d.	138	109	103
claw: length	n. d.	43	37	31
basal segment: max. height	n. d.	42	43	35
basal segm.: anterior height	n. d.	n. d.	21	17
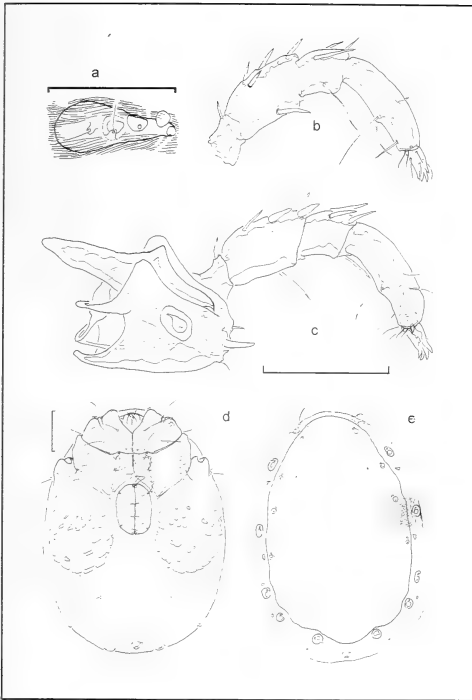
FIG. 40. *Utaxatax brahmeri* sp. nov. (male): (a) eye plate, (b) palpus (slide 13/93-1), (c) gnathosoma, chelicera, palpus (slide 13/93-2), (d) VS (slide 13/93-1), (e) DS (slide 13/93-1). Scale bars = 100 μm.

Derivatio nominis. With respect to Shri Buddadeb Chattopadyaya, who showed me the first steps into "Brahmeri-painting," a traditional meditative Indian style of painting.

Discussion. The sampling spots of the two sexes (4 males from Darjeeling and one female from Himachal Pradesh) are situated in the Himalayas more than 1000 km apart from each other. Despite some minor differences (e.g., in the shape and chaetotaxy of the palp) the female is tentatively assigned to this species. For a more reliable decision males and females from both areas should be available.

Utaxatax (s.s.) *brahmeri* differs from all other known species of the subgenus in that C4 extends about 100 μm posterior to the genital field. The only other species of the subgenus in which C4 extends more than 50 μm posterior to the genital field is *U. ovalis*. *U. ovalis* differs from *U. brahmeri* in that there are only three pairs of glandularia included in the dorsal shield in the former and 4 in the latter species.

TABLE 20. *Utaxatax brahmeri* sp. nov. 2: Palpal data [measurements in μm].

Collection-No. (Specimen) sex [m = male]	*U. brahmeri* 13/93 spec. 1 m
P1-length	25.3
P1-height	27
P1-length/height ratio	0.94
P1: % of total length	9.5 %
P2-length	76
P2-height	41
P2-length/height ratio	1.85
P2: % of total length	28.4 %
P3-length	44
P3-height	34
P3-length/height ratio	1.29
P3: % of total length	16.5 %
P4-length	92
P4-height (incl. hook)	29
P4-length/height ratio	3.17
P4: % of total length	34.4 %
P5-length	30
P5-height	15
P5-length/height ratio	2.00
P5: % of total length	11.2 %
Palpus: total length	267.3
length ratio P2/P4	0.8
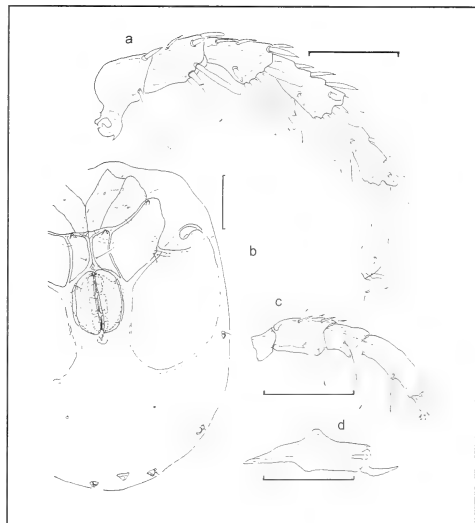
FIG. 41. *Utaxatax brahmeri* sp. nov. (female): (a) IV-L (slide '95/147), (b) VS (slide '95/147), (c) palpus (slide '95/147), (d) chelicera (slide '95/147). Scale bars = 100 μm.

Utaxatax (s.s.) *crassipalpis* sp. nov.

Holotype: 1 female adult from collection "1995-05-31 [13/93]" (muddy detritus from a spring in a bamboo forest; on trek from Phalut to Gorkhey after 1200m; Darjeeling, India).
Holotype in the NMB.

Description of females. Characters as given in the definition and inventory for the subgenus *Utaxatax.* DS with postocularia and 4 pairs of glandularia; eye-lenses on platelets; palps "mamersopsid-like"; C4 hardly extending posterior to the GF. No major differences between *U. parvati* and *U. ventriplax* (Gerecke 1988, Figs. 4, 5) regarding leg chaetotaxy.
Males, Nymphs and larva. Unknown
Habitat. Discovered in a spring in a bamboo forest in 3450 m a.s.l.
Distribution. Known only from the type locality below the peak of Mount Phalut in the eastern Himalayas (Darjeeling, India).
Derivatio nominis. With reference to the "mamersopsid-like" stocky palp of the species.
Discussion. Utaxatax (s.s.) *crassipalpis* is the only known species of the genus with a "mamersopsid-like" palp.
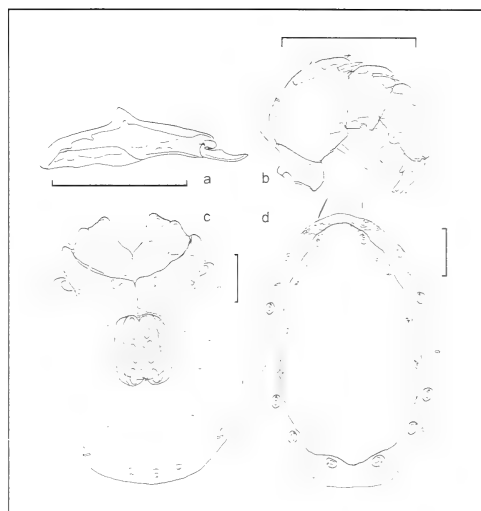
FIG. 42. *Utaxatax crassipalpis* sp. nov. (female): (a) chelicera (slide 13/93), (b) palpus (slide 13/93), (c) VS (slide 13/93), (d) DS (slide 13/93). Scale bars = 100 µm.

TABLE 21. *Utaxatax* 3: Idiosoma [measurements in µm], n.d. = not dissected.

	U. crassipalpis	*U. parvati*	*U. gereckei*	
Collection	13/93	7/93	`95/43	`95/82
sex	female	female	female	female
Dorsal shield (DS): length	477	509	385	374
Dorsal shield: width	291	325	260	253
DS: length/width	1,64	1,57	1,48	1,48
No. of glandularia in DS	4	4	4	4
Postocularia: medial - lateral	l	m	m	m
Eye platelets	n. d.	n. d.	n. d.	n. d.
median distance	28	n. d.	n. d.	n. d.
length	76	n. d.	n. d.	n. d.
Coxae				
median length C3	54	61	56	49
length suture C1/C1	54	40	38	43
left to right width C3 /C3	290	262	213	211
left to right distance Cg4	115	81	56	56
paramedian suture C3: lgth.	88	83	67	74
posterior margins: GF to C4	22	27	34	29
Genital field (GF)				
GF to end of body	213	187	156	85
genital opening: width	103	90	76	81
genital opening: length	126	128	108	112
gen. opening: length/width	1,22	1,42	1,42	1,38
genital flaps: length	150	134	112	112

TABLE 22. *Utaxatax* 4: *U. crassipalpis*. Palpal data [measurements in μm].

Collection sex:	U. crassipalpis 13/93 female
P1-length	23
P1-height	35
P1-length/height ratio	0.67
P1: % of total length	9.9
P2-length	81
P2-height	58
P2-length/height ratio	1.41
P2: % of total length	34.8
P3-length	35
P3-height	47
P3-length/height ratio	0.73
P3: % of total length	14.8
P4-length	58
P4-height (incl. hook)	33
P4-length/height ratio	1.73
P4: % of total length	24.7
P5-length	37
P5-height	17
P5-length/height ratio	2.13
P5:% of total length	15.8
Palpus: total length	232.8
length ratio P2/P4	1.4

Similar to the situation in *Bandakia* and *Stygomamersopsis*, there are now also *Utaxatax* species with both types of palps ("anisitsiellid-" and "mamersopsid-like").

Utaxatax (s.s.) *gereckei* sp. nov.

Holotype: 1 female adult from collection "1995-06-16 [`95/43]" (Kunoi-Nala, 25 min trek upstream from Kahknal, Kullu Valley, Himachal Pradesh, India). Paratype: 1 female adult from collection "1995-06-26 [`95/82]" (Kunoi-Nala, 30 min trek upstream from Kahknal, Kullu Valley, Himachal Pradesh, India).
Type material in the NMB.

Description of females. Characters as given in the definition and inventory for the subgenus Utaxatax and as shown in Fig. 43. DS with postocularia and 4 pairs of glandularia; eye-lenses on platelets; palps "anisitsiellid-like"; C4 hardly extending posterior to the GF. All legs, but especially IV-L, with segments very stocky and short and with a high number of strong setae (measurements are given in Table 21).

FIG. 43. *Utaxatax gereckei* sp. nov.: (a) palpus, (b) chelicera, (c) eye plates, (d) IV-L. Scale bars = 100 μm.

Males, Nymphs and larva. Unknown
Habitat. Discovered in cascades with mosses, at 2000 m a.s.l., in two locations, in a second order mountain stream.
Derivatio nominis. With respect to R. Gerecke and his outstanding contributions to water mite research.
Discussion. U. gereckei sp. nov. differs from all other known species of the genus in having a IV-L with extremely stout segments and thick setae.

Utaxatax (s.s.) *parvati* sp. nov.

Holotype: 1 female adult from collection "1993-05-30_1 [7/93]" (spring brook, 2,5h trek from Sandakphu towards Sarbakum-Phalut, Darjeeling, India).
Holotype in the NMB.

Description of female. Characters as given in the definition and inventory for the subgenus Utaxatax. DS with postocularia and 4 pairs of glandularia; eye-lenses on platelets; palps "anisitsiellid-like"; C4 extending posterior to the GF for approx. 30 μm, which is about the length of an acetabula (measurements are given in Table 21). No major differences between *U. parvati* and *U. ventriplax* (Gerecke 1988, Figs. 4, 5) regarding leg chaetotaxy.
Males, Nymphs and larva. Unknown.
Habitat. Discovered in a spring brook at 3500 m a.s.l.
Distribution. Known only from the type locality in the eastern Himalayas (spring brook, after 2,5 h trek from Sandakphu towards Sarbakum-Phalut, Darjeeling, India).
Derivatio nominis. With reference to the goddess Parvati, known in the Hindu pantheon as a feminine appearance of the god Shiva. Shiva spread his hair to form the Himalayas and rescued in this way the world from being destroyed by the furious goddess Ganga.

Discussion. Utaxatax (s.s.) *parvati* is most closely related to *U. brahmeri*. However, the two species are clearly different in that C4 extends only about 30 µm posterior to the genital field in the former and about 100 µm in the latter species.

Subfamily Bharatoniinae (subfam. nov)

Diagnosis for adults. Characters of the family Limnesiidae.
Genital field with three pairs of acetabula in two rows. The two anterior pairs of acetabula are elongated and spread along the medial border of the genital flaps. Acetabula of each side form a belt-like strip and are close to or adpressed to the outer medial border of the genital flaps, but not completely fused to it. Surface of acetabula parallel or at right angles to the medial outer surface of the genital flaps. In the latter cases, the surface of the first two pairs of acetabula is (1) parallel to the surface of the ventral shield if the flaps are wide open, and (2) at right angles to the surface of the ventral shield (and facing each other) if the flaps are closed. The third pair of acetabula is less elongated, more roundish and - regardless of whether the genital flaps are open or closed - parts of its surface are pointing posteriorly. Either the third and the two anterior acetabula are fused by their enlarged basal sclerites, with the third acetabulum forming the posterior end of the strip stretching along the medial border of the genital flap, or the basal sclerites of the anterior two pairs are small, and those acetabula are lying free in the integument (while the third acetabula appear to lie on the posterior outside (!) surface of the genital flaps).

Male genital skeleton short, similar to those found in several early derived taxa of Limnesiidae.

Chelicerae with typical shape: distal end of cheliceral claw bent strongly dorsally and proximal end of basal segment bent strongly ventrally (Fig. 45).

Palp five-segmented; P5 long, P4 with or without tubercles on the ventral surface, P3 with or without ventral projection, P2 with strong ventral seta, this seta with or without tubercle, P1 with dorsal seta present.

Eye-region with a typical set of platelets and segmental remnants as shown in Fig. 48. Lenses of each side on a small separate platelet to which only a slit-organ is fused laterally. Dorsomedial to it a platelet with a glandularium and a seta and medially a platelet with a second glandularium. This medial platelet may be adpressed to a nasal plate which arches above the gnathosoma.

Dorsum with one large posterior and another large anterior shield. Lateral to the furrow between these two shields, there are (1) two small platelets and glands in females, or (2) free glands only in nymphs, or (3) these platelets and glands are sometimes fused to the posterior plate in males. Dorsal glands all free in females (and nymphs) but some of them fused to the dorsal shields in males.

Ventral shield complete in males and absent in females. However, in females secondary sclerotization arising from the C4, the postgenitale, and the excretory pore plate does increase the chitinized part of the body wall (Fig. 46).

Organization of coxal plates with C1 extending from the gnathosoma directly up to the pregenital plate; parts of C4 overlapping medial parts of C3 (and in some cases over parts of C2) and Cg4 found either at the anteromedial border of C3 or laterally from the center of C2.

IV-L-6 always with well-developed claws and an elongated seta which is about as long as the claw. Claws of I-III-L in some cases do have a dorsal clawlet and are otherwise either hook-like or equipped with ventral blade and clawlet.

Diagnosis of nymphs. Characters of the family Limnesiidae. Basal sclerites of the two pairs of acetabula fused with homologs of the genital flaps forming a triangular plate in the provisory genital field; the plate is about twice the length of the acetabulum (Fig. 47).

Ventral shield absent. Fourth coxae slightly enlarged by lateral and posterior secondary sclerotizations and always with medial part of the fourth coxae projecting anteriorly and overlapping the medial part of the third coxae. Cg4 situated in the anterolateral edge of this projection. Dorsum without complete dorsal shield, but with two larger plates and two small platelets lateral to the furrow between them.

Other characters similar to adults, but secondary sclerotization less expressed.

Larva. Unknown

Discussion. The subfamily Bharatoniinae includes the two monotypic genera *Bharatonia* and *Shivatonia* (gen. nov.). With the high number of synapomorphic character states in the adult morphology, and the characteristic gradual differentiation the organization of the genital field, the new genus from the Himalayas, *Shivatonia,* may be considered an intermediate character state in a transformation series leading from a *Nilotonia*-like situation to the organization of the acetabula found in other early derived taxa of the

Limnesiidae, especially *Neomamersa, Meramecia* and *Neotorrenticola* as apomorph.

The plesiomorphic condition is expressed in *Nilotonia* species, with their acetabula lying free in the gonopore without enlarged basal sclerites. Fusion of enlarged basal-sclerites to a common strip situated on each side of the gonopore below the movable flap is an apomorphic character state found for example in *Dartia boettgeri*. In *Shivatonia* this strip is raised and adpressed to the medial border of the genital flap, while in *Neomamersa conjuncta* it is fused to the medial border of the genital flap, with the setae still arising from the "old" medial border of the flap (now lateral to the fused basal sclerites of the acetabula).

Bharatonia shows a situation where the basal sclerite of the third acetabulum is already fused to the posterior end of the genital flap, while the two anterior pairs are still situated well medial and "inside" the flaps. If the anterior acetabula pairs developed enlarged basal sclerites, adpressed to the medial border of the genital flap, the situation found in *Shivatonia* is reached. If in addition the acetabula proliferated, a situation is reached exactly as it is found in *Neotorrenticola* (Neotorrenticolinae, Limnesiidae).

The gradual changes in the organization of the genital region go along with several other character states in adult and nymphal morphology connecting Bharatoniinae closely to other subfamilies of the Limnesiidae (e.g., the short genital sclerite found in *Bharatonia* and *Shivatonia* is similar to the one depicted for *Neomamersa* but clearly different from the ones described for *Nilotonia, Bandakia* and *Limnesia*). A revision of the early derived subfamilies of the Limnesiidae would be the next step to decide if the transformation series in the organization of the genital field can be related to other synapomorphic character states in a phylogenetic analysis.

Genus: *Bharatonia* Cook, 1967 [1 sp.]

Typus generis: *Bharatonia vietsi* Cook, 1967. Material examined: *Bharatonia vietsi* paratype, male, slide 3997 SMF; *Bharatonia vietsi*, slide from "1990-8-24[Solan]", CAP [new record]. Location of types: holotype: CNM; paratypes: as holotype and in SMF

Definition (adults)

Characters of the subfamily Bharatoniinae as defined above and:

• Two rows of 3 acetabula. Anterior two acetabula of each row form a strip along the medial border
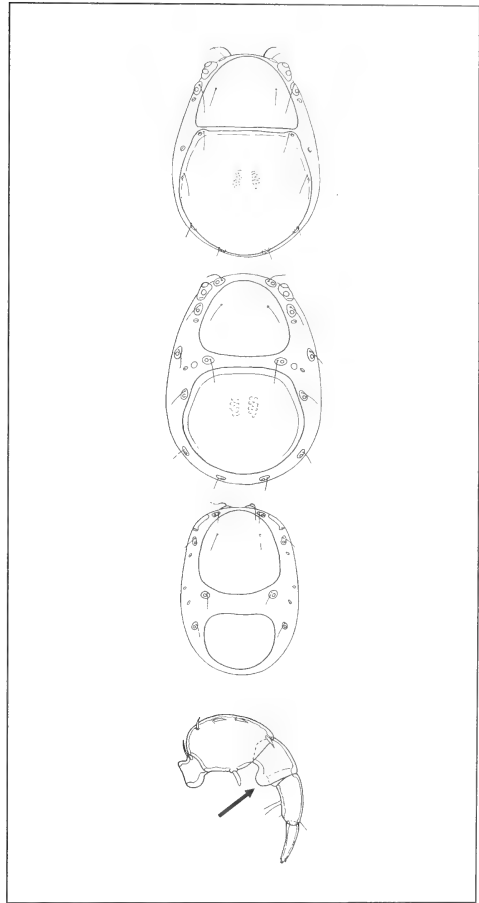
FIG. 44. *Bharatonia vietsi*: Dorsal views of male (top), female (upper middle) and nymph (lower middle) and lateral view of palpus (male) with round protrusion at P3 medially (bottom) [Figs. from Cook (1967)].

of the movable genital flap, but situated at right angles to the medial outer surface of the flap; anterior two acetabula without enlarged basal sclerites; third acetabulum less elongated more oval in shape, and fused to the posterior outer surface of the movable genital flap (Fig. 45).

Species included

Bharatonia vietsi Cook, 1967 is the only known species of the genus. Cook (1967) collected males, females and nymphs in a seepage area of the Western Ghats (Maharashtra State, India).

Inventory (adults)

DS/VS. Dorsum with one large posterior and another large anterior shield. In females (and nymphs) two small platelets are found lateral to the furrow between the two large shields, in males they are fused to the posterior shield. In females (and nymphs) all dorsal glands free and not fused to the DS, in males two (or three) pairs of dorsal glands fused to the posterior dorsal shield. Postocular setae always situated in semi-lateral position on the anterior dorsal shield. VS complete in males, not so in females. However, more than 50% of the ventral surface of the adult female is stabilized by chitin due to the primary sclerotization of the coxal plates and due to secondary sclerotization (1) at the medial and posterior borders of C4, (2) at the postgenitale, (3) around the pair of glands posterolateral to the GF, and (4) around the excretory pore. (In the nymphs the very same secondary sclerotizations are found but they are much smaller in extent.)
Eye-region. As given in the description of the subfamily.
Coxae. Organization of coxal plates with C1 extending from the gnathosoma up to the pregenital plate; medial parts of C4 overlapping medial parts of C3 (and in some cases parts of C2). Suture C3/C4 incomplete.
Cg4. Cg4 is situated near mid-length of suture C2/C3 on C3. The Cg4 is found on the lateral edge of a protrusion of the C4 which covers the medial third of C3.
Ac. See definition.
GF. Pre- and postgenitale enlarged in females and fused to secondary sclerotization of C4 (forming a complete ventral shield) in males. Posterior border of C4 at same level as posterior border of genital flaps. Insertions of IV-L at level of anterior half of genital field.
I-L-6. I-L-6 with a few hairs and ventrally with a few very short setae. Claws with blade and ventral and dorsal clawlet.
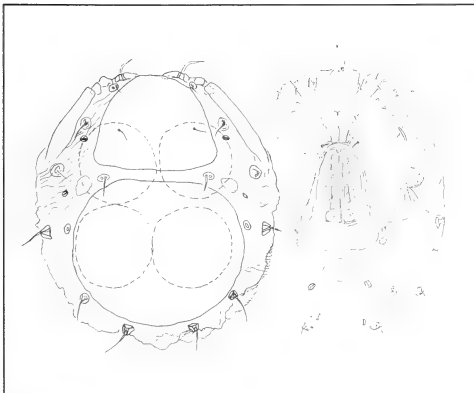*IV-L-6.* IV-L-6 always with well-developed claws and an elongated seta which is about as long as the claws. Claws similar to those on I-L-6 but blade less developed.
Palpus. Palpus with P5 long, P4 with ventral protrusions small, P3 showing sexual dimorphism (see Fig. 44 and Fig. 45), P2 with a blunt and slightly curved thick seta on its ventral surface and P1 with dorsal seta present.
Chelicerae. Cheliceral claw strong with the tip of the claw bent dorsally. Basal segment with dorsal surface
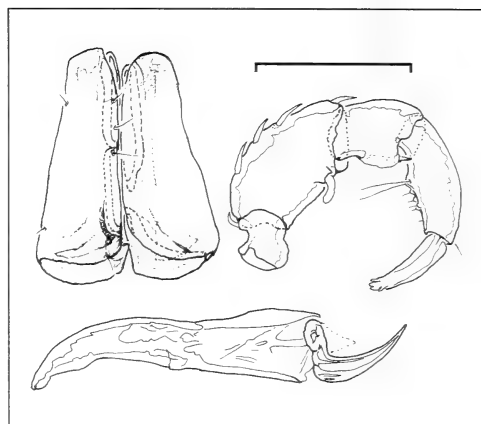
FIG. 45. *Bharatonia vietsi* (paratype female, slide 3997, SMF): Top left: genital field with aberrant number of two Ac on left side; genital flaps closed and acetabula with their surfaces facing each other. Top right: palpus (with P3 ventrally blade-like). Bottom: chelicera. Scale bar = 100 μm.

without strong elevation and with its proximal end bent strongly ventrally. Chelicerae with total length 245–270 μm and cheliceral claw approx 47 μm in length.

Further remarks

Nymphs. See under description for the subfamily.
Larva. Unknown.
Habitat. Known from seepage area only.
New record. The species was discovered for the second time during investigations for the present study. A single male was found – 1500 km north of the locus typicus – in a seepage aerea at 2500 m a.s.l. in the Solan Valley (near Manali, side valley of the Kullu Valley, H.P., India. Collection: "1990-8-24 [Solan]").
Distribution. Locus typicus in the Westen Ghats, in Maharashtra State (India) and in the southern Himalayas, as given above.

Genus: *Shivatonia* gen. nov. [1 sp.]

Typus generis: *Shivatonia acetabulensis* sp. nov.; Material examined: Type series, NMB. Location of types: Holotype: NMB; paratypes: as holotype and in ZSI

Definition (adults)

Characters of the subfamily Bharatoniinae as defined above and:

- Two rows of 3 acetabula, each on a secondary sclerotization, adpressed but not completely fused to the medial outer border of the movable genital flaps. Secondary sclerotization formed by the enlarged and fused basal sclerites of the acetabula. Hence: acetabula neither below genital flaps (as in Bandakiinae, Anisitsiellinae) nor fused "onto" the genital flaps (as in most other Limnesiidae).

Derivatio nominis

This genus *Shivatonia* gen. nov. hopefully helps to modify the old approach to the Anisitsiellidae-Limnesiidae complex and opens the field to new concepts. Similarly, in one of his aspects the Hindu god Shiva is the one who allows progress and perpetuation through destruction. The suffix "-tonia" is often used as suffix in the "anisitsiellid-like" mites.

Species included

Shivatonia acetabulensis sp. nov. is the only known species of the genus. Nymphs, males and females were collected from mosses in two brooklets situated a few kilometers from each other near Rimbik (Darjeeling, India. Coll.: 1993-06-02_1, 1993-06-02_2).

Inventory (adults):

DS/VS. Dorsum with one large posterior and another large anterior shield. Organization of plates, glands and setae in dorsal and ventral shields with differences between males, females and nymphs as given for *Bharatonia* and in the description of the subfamily. In

FIG. 47. *Shivatonia acetabulensis* sp. nov. (nymph): Ventral view.

males VS complete; in females (and nymphs) not complete VS, but more than 50% of the ventral surface of the adult female is stabilized by chitin, due to the primary sclerotization of the coxal plates and to secondary sclerotization (1) at the medial and posterior borders of C4, (2) at the postgenitale, (3) around the pair of glands posterolateral to the GF, and (4) around the excretory pore. (In the nymphs the very same secondary sclerotizations are found but they are much smaller in extent).

Eye-region. As given in the description of the subfamily.

Coxae. Organization of coxal plates with C1 extending from the gnathosoma up to the pregenital plate; medial parts of C4 overlapping medial two-thirds of C3 and posterior parts of C2. Sutures C2/3 and C3/C4 incomplete.

Cg4. Cg4 is situated in the lateral half of C2. The Cg4 is found on the lateral edge of a finger-like protrusion arising from C4, which covers the medial parts of C3 and posteromedial parts of C2.

Ac. See definition.

GF. Pre- and postgenitale enlarged in females and fused to secondary sclerotization of C4 (forming a complete ventral shield) in males. Posterior border of C4 at same level as posterior border of genital flaps. Insertions of IV-L at level of mid-length of genital field.

I-L-6. I-L-6 with a few hairs and ventrally with a few very short setae. Claws with blade and ventral and dorsal clawlet.

FIG. 46. *Shivatonia acetabulensis* sp. nov. (female). Right: dorsum. Left: venter.
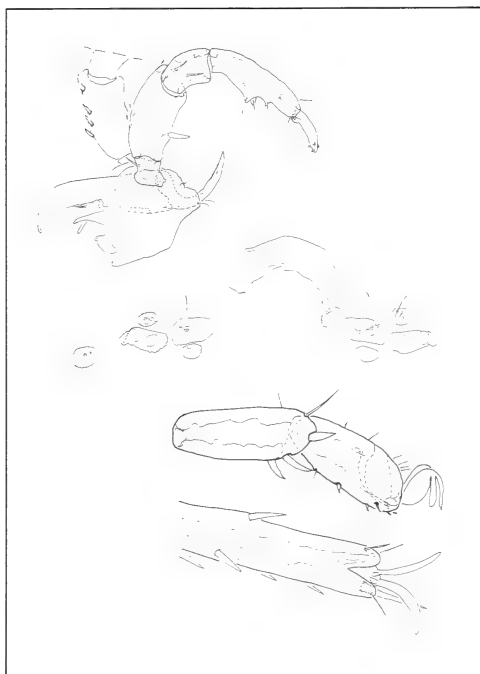
FIG. 48. *Shivatonia acetabulensis* sp. nov. (female). Top: gnathosoma, palpus and chelicerae. Middle: organization of eye plates and nasal plate. Bottom: I-L-5,6 and tip of IV-L-6.

IV-L-6. IV-L-6 always with well-developed claws and an elongated seta which is about as long as the claws. Claws similar to those on I-L-6 but with out clawlets and with ventral blade much less developed.
Palpus. Palpus with P5 long, P4 with large ventral protrusions (as found in some members of the Nicalimnesiinae), P3 with four dorsal setae, P2 with a short, thick and pointed seta on its ventral surface and P1 with dorsal seta present.
Chelicerae. Cheliceral claw extremely strong with the tip of the claw bent dorsally beyond the level of the dorsal border of the basal segment. Dorsal border of basal segment without elevation and with its proximal end bent strongly ventrally. Chelicerae with 220–260 µm total length.

Taxonomic placement

The palpus of *Shivatonia* gen. nov. differs from palps of the Anisitsiellinae and Bandakiinae in having a long P5, strong ventral tubercles on P4 and a thick ven-

tral seta on P2. A similar palpus shape is found in the subfamily Nicalimnesiinae. In *Nicalimnesia andha*, P5 is even more elongated and the ventral tubercles on P4 are even more prominent. The palpus, however, differs from that of the Nicalimnesiinae in having well-visible claws at the tip of P5, and in having a dorsal seta on P1. The shape of the chelicerae is striking because of their extremely strong claw, which is bent upwards beyond the level of the dorsal border of the basal part. The secondary sclerotization, adpressed to the medial border of the genital flaps carrying 3 acetabula each, expresses a plesiomorphic character state if compared with the situation in Nicalimnesiinae, where the basal sclerite of the acetabula is completely fused to the movable genital flaps (female), or to the genital plate formed by the basal sclerite and the homologs of the genital flaps (male). The character state expressed in *Shivatonia* is apomorphic if compared with species of *Dartia* (*Nilotonia*, Nilotoniinae), where the basal sclerites of the acetabula are clearly enlarged and fused to each other in several cases, but never adpressed or fused to the genital flaps or their homologs.

Shivatonia acetabulensis sp. nov.

Holotype: 1 female adult from collection "1993-06-02_1 [22/`93]" (forest brook, 2 km from Gorkey to Ramam, Darjeeling, India). Paratypes: 1 male, 2 females, and 1 nymph with same data as holotype [1 of these females used for e-microscopy]; 1 female adult from collection "1993-06-02_2 [22/`93]" (forest brook, 3 km from Gorkey to Ramam, Darjeeling, India).
Type material placed in the NMB. A parataype will be deposited in the ZSI (India).

Description of adults and nymphs. As given in the generic description and shown in Figs. 46–49. Measurements are given in Table 23 and Table 24
Larva. Unknown.
Habitat. As given in the generic description.
Derivatio nominis. With reference to the acetabula being in an intermediate position between the former Anisitsiellidae and Limnesiidae.

Subfamily Anisitsiellinae, Koenike 1910 (stat. nov.)

The inclusion of 22 genera with 80 species (Table 25) in the Anisitsiellinae (stat. nov.) is suggested. Among the species discussed below there are three new to science. Several genera are only tentatively assigned
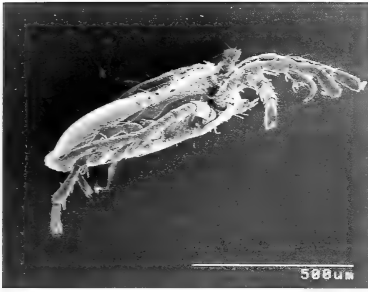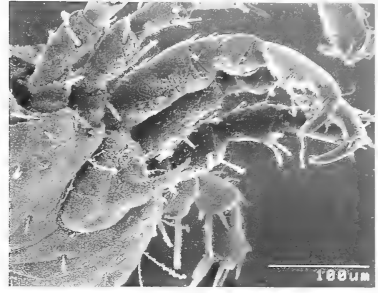
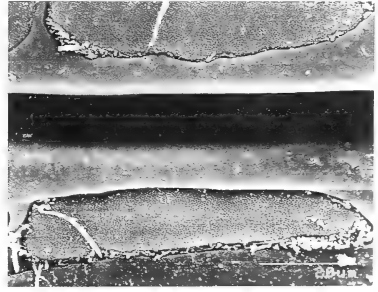FIG. 49. *Shivatonia acetabulensis* sp. nov. (female): (1) lateral view, (2) semi-anterior view of ventral shield, gnathosoma and palpi, (3) anterior view, (4) dorsal view, (5) tip of IV-L-6, (6) genital field, detail of second pair of acetabula, (7) genital field in semi-lateral view.

TABLE 23. *Shivatonia acetabulensis* sp. nov. 1: Idiosoma [measurements in µm].

Shivatonia acetabulensis sp. nov.	Holotype	Paratype	
Collection	22/93	22/93	21/93
(Specimen number)	(1)	(2)	
sex [m = male; f = female]	f	m	f
Idiosoma / Dorsal shields			
excretory pore plate length	63	67	60
excretory pore plate width	102	121	100
anterior dorsal shield: length	220	220	228
anterior dorsal shield: width	300	284	312
posterior dorsal shield: length	360	323	350
posterior dorsal shield: width	400	357	397
Coxae			
left to right width C3	360	312	347
left to right distance Cg4	210	172	202
Genital field (GF)			
genital opening: width	127	102	127
genital flaps: length	200	167	197
genital opening: length/width ratio	1,57	1,64	1,55
length of 1st, 2nd and 3rd acetabulum	78/65/30	67/65/27	78/65/32
postgenital plate, medial length	55	59	57
postgenital plate, max. width	205	198	208
Chelicera			
basal segment: length	187	137	175
basal segment: height	50	52	52
basal segment: length/height ratio	3,74	2,63	3,37
claw: length	103	82	-
claw: height	50	52	52
claw: length/height ratio	2,06	1,58	-
total length of chelicera	255	218	-

to the subfamily as a knowledge of larval or nymphal stages would be necessary to confirm their placement.

In a first step, Anisitsiellinae are divided into five genera-groups (*Nilotonia*-group, *Anisitsiellides*-group, *Platymamersopsis*-group, *Mamersides*-group, and *Mahemamersides*-group). These are based on the constancy in the shape of the chelicerae, which goes along with other character states shared by the members of a group. Four genera are only tentatively assigned to the subfamily and placed as genera incertae sedis. The following table shows the grouping of the genera and their former position.

It should be avoided raising these groups to a phylogenetically significant taxonomic state at present. The consequent next step is the revision of the other subfamilies of the Limnesiidae. This revision should show if the genera placed incertae sedis can be included in other Limnesiidae subfamilies.

Diagnosis for adults. Characters of the Limnesiidae, and typically with three pairs of acetabula situated in two rows below movable genital flaps (proliferation is possible in individual specimens; one species with 12–16 instead of 3 acetabula in a row). Acetabula with basal ring sclerites enlarged in one subgenus (*Dartia*), but the enlarged basal sclerites never adpressed to the medial border of the genital flaps (as in Bharatoniinae). IV-L in all but one species (*Sigthoriella hygropetrica*) without claws. P2 with ventral seta present in all but two species with aberrant palps (*Anisitsidartia micropalpis, Psammotorrenticola gracilis*). If a dorsal elevation is present on the dorsal surface of the basal

segment of the chelicera, than this elevation is proximal or rounded, but never pointed (as in Bandakiinae).
Diagnosis for larva. As discussed under the family Limnesiidae.

Platymamersopsis-group

Three genera (*Platymamersopsis, Paddelia, Gilatonia*) are included in this group of genera.

Description for adults. Chelicera "*Platymamersopsis*-like" (Fig. 50); VS complete; DS complete or divided into 2-3 large plates covering most of the dorsal surface (Fig. 53, Fig. 55); P2 typically with a strong claw; dorsal furrow narrow; lateral eyes fused with the ventral shield; swimming hairs absent but IV-L-6 lacking claws and shortened and in several species flattened.

TABLE 24. *Shivatonia acetabulensis* sp. nov. 2: Palpi, legs [measurements in μm].

S. *acetabulensis* sp. nov. Collection: (Specimen number)	Holotype 22/93 (1)		Paratype 22/93 (2)		21/93	
Palpal segments						
P1-length	33	33	33	34	35	-
P1-height	44	45	36	37	38	-
P1-length/height ratio	0,75	0,73	0,91	0,91	0,92	-
P1: % of total length	7,47	7,42	8,55	8,83	8,10	
P2-length	131	133	113	112	129	135
P2-height	64	62	53	50	59	-
P2-length/height ratio	2,05	2,15	2,13	2,24	2,19	-
P2: % of total length	29,64	29,89	29,27	29,09	29,86	
P3-length	75	76	65	64	73	-
P3-height	47	48	42	40	45	-
P3-length/height ratio	1,60	1,58	1,55	1,60	1,62	-
P3: % of total length	16,97	17,08	16,84	16,62	16,90	
P4-length	142	143	123	123	137	-
P4-height (incl. hook)	47	48	35	36	43	-
P4-height (minimum)	27	27	24	25	27	-
P4-length/height ratio*	3,02	2,98	3,51	3,42	3,19	-
P4: % of total length	32,13	32,13	31,87	31,95	31,71	
P5-length	61	60	52	52	58	-
P5-height	20	18	18	17	18	-
P5-length/height ratio	3,05	3,33	2,89	3,06	3,22	-
P5:% of total length	13,80	13,48	13,47	13,51	13,43	
Palpus: total length	442	445	386	385	432	-
length ratio P2/P4	0,92	0,93	0,92	0,91	0,94	
Legs: dorsal length						
L1	95	97	95	99	98	-
L2	75	75	72	71	78	-
L3	88	91	78	78	90	-
L4	130	137	118	119	137	-
L5	165	165	143	150	167	-
L6	156	152	138	146	150	-
Legs: total length	709	717	644	663	720	-
L6: terminal seta	26	27	29	27	27	
L6: claw	28	28	25	25	29	

* length/height ratio with height including hook

TABLE 25. Genera included in the *Anisitsiellinae* stat. nov.

Genus	no. of spp.	Genus group	Former position
1. *Gilatonia*	1	*Platymamersopsis*	Anisitsiellinae
2. *Paddelia*	1	*Platymamersopsis*	nov. gen.
3. *Platymamersopsis*	12	*Platymamersopsis*	Anisitsiellinae
4. *Hydrobaumia*	1	*Mamersides*	Anisitsiellinae
5. *Mamersides*	2	*Mamersides*	Anisitsiellinae
6. *Mamersopsides*	2	*Mamersides*	Anisitsiellinae
7. *Mamersopsis*	3	*Mamersides*	Anisitsiellinae
8. *Navamamersides*	1	*Mamersides*	Anisitsiellinae
9. *Mahamamersides*	1	*Mahemamersides*	Anisitsiellinae
10. *Nilgiriopsis*	1	*Mahemamersides*	Anisitsiellinae
11. *Anisitsiellides*	11	*Anisitsiellides*	Anisitsiellinae
12. *Sigthoreilla*	1	*Anisitsiellides*	Anisitsiellinae
13. *Zelandatonia*	1	*Anisitsiellides*	Nilotoniinae
14. *Anisitsidartia*	1	*Nilotonia*	Anisitsiellinae
15. *Anisitsiella*	2	*Nilotonia*	Nilotoniinae
16. *Mamersella*	2	*Nilotonia*	Anisitsiellinae
17. *Nilotonia*	41	*Nilotonia*	Nilotoniinae
18. *Rutacarus*	5	*Nilotonia*	Nilotoniinae
Manotonia	2	subg. within *Nilotonia*	Nilotoniinae
Mamersellides	0	syn. of *Anisitsiella*	Nilotoniinae
19. *Psammotorrenticola*	1	*incertae sedis*	Anisitsiellinae
20. *Ranautonia*	1	*incertae sedis*	Nilotoniinae
21. *Sigthoria*	1	*incertae sedis*	Anisitsiellinae
22. *Stygomamersopsis*	2	*incertae sedis*	Anisitsiellinae

Genus: *Platymamersopsis* Viets, 1914 [12 spp.]

Typus generis: *Platymamersopsis nordenskiöldi* Viets, 1914

Material examined: *Platymamersopsis agnevi* holotype, slide, SMF; *Platymamersopsis chutteri* holotype, slide 6857, SMF; *Platymamersopsis cooki* holotype, slides 3913, 3914, SMF; *Platymamersopsis mysorensis* paratype, slide 3981, SMF; *Platymamersopsis similis* paratype, slides 4050, 4051, SMF; *Platymamersopsis vietsi* paratype, slide 4061, SMF. Location of genotype: SMF

Definition (adults)

Characters of the Anisitsiellinae as defined above and:
- Typical shape of chelicerae as in figure Fig. 50.
- VS and DS complete. In *Platymamersopsis* (s.s.) DS with a peripheral ridge (Fig. 50); in *P.* (*Neomamersella*) dorsal furrow wide with many glandularia (Fig. 51).
- In *Platymaersopsis* (s.s.) the Cg4 is situated medially on C3 well lateral of the midline (Fig. 50); in *P.* (*Neomamersella*) Cg4 is absent.

Subgenera and species included

The members of the *Platymamersopsis* (s.s.) are morphologically very similar to each other. Since the discussion of the genus by Cook (1974), two more species of *Platymamersopsis* (s.s.) have been described, both from Africa (Viets 1982), leading to the 11 species currently known to science. I propose to shift the subgenus *Neomamersella* from *Mamersella* to *Platymamersopsis*. Among the characters separating the subgenus *Neomamersella* from *Mamersella* and connecting it with *Platymamersopsis* are (1) the medial fusion of C3/C3, (2) the ridge leading anteriorly from the insertions of IV-L towards the insertions of III-L, (3) the +/– rectangular shape of C4, and (4) the chaetotaxy of the palp with a strong and long seta on the ventral side of P2. In this concept the subgenus *Neomamersella* would be a less sclerotized form with dorsal furrow wide, compared to the highly sclerotized *Platymamersopsis* (s.s.) with its narrow dorsal furrow.

A list of the accepted species (and notes on their distribution) is given below.

(1) *P.* (s.s.) *agnevi* Viets, 1982 (Africa)
(2) *P.* (s.s.) *adhika* Cook, 1967 (India, Mysore)
(3) *P.* (s.s.) *chutteri* Viets, 1982 (Africa)
(4) *P.* (s.s.) *cooki* Viets, 1970 (Africa)
(5) *P.* (s.s.) *crassipes* Cook, 1966 (Africa, Liberia)
(6) *P.* (s.s.) *liberiensis* Cook, 1966 (Africa, Liberia)
(7) *P.* (s.s.) *mysorensis* Cook, 1967 (India, Mysore)
(8) *P.* (s.s.) *nordenskiöldi* Viets, 1914 (Africa, Cameroon, Liberia)
(9) *P.* (s.s.) *ovalis* Cook, 1966 (Africa, Liberia)
(10) *P.* (s.s.) *similis* Cook, 1966 (Africa, Liberia)
(11) *P.* (s.s.) *vietsi* Cook, 1966 (Africa, Liberia)
(12) *P.* (*Neomamersella*) *tototaensis* (Cook, 1966) (Africa, Liberia)

Inventory (adults)

DS/VS. See definition.

Eyes. Anterior and posterior lenses fused to ventral shield in *Platymamersopsis* (s.s.); posterior pair free in dorsal furrow in subgenus *Neomamersella*.
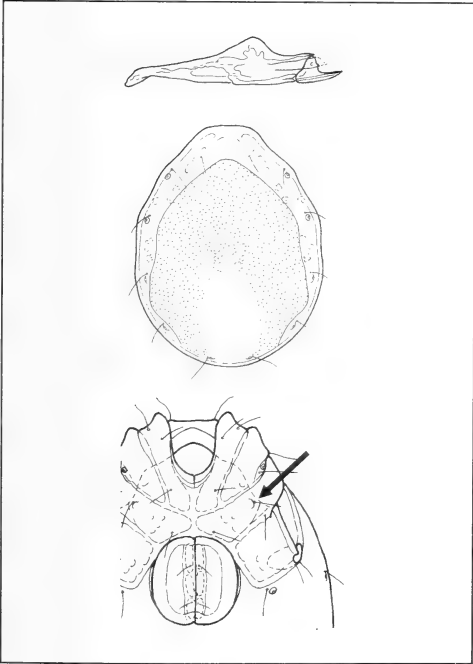
FIG. 50. *Platymamersopsis* (s.s.) *mysoriensis* Cook, 1967. Top: chelicerae. Middle: dorsal shield. Bottom: coxae with Cg4. [Figs. middle and bottom from Cook (1967), partly modified].
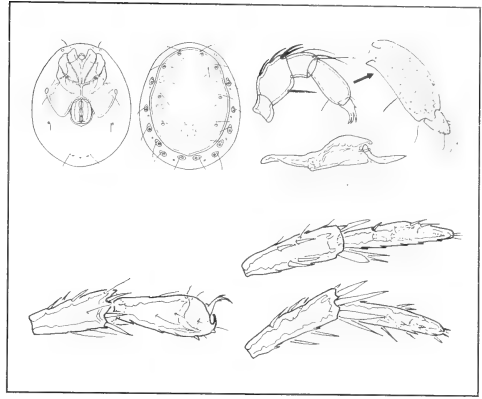
FIG. 51. *Platymamersopsis* (*Neomamersella*) *tototaensis*. Top: (from left to right) VS, DS, palpus and chelicera. Bottom: I-L-5,6; left and right IV-L-5,6.

Coxae. Anterior border of C3 concave; C3/C3 and anterior part of C4/C4 fused medially; C4 more or less rectangular.

Cg4. See definition.

GF. C4 closely impending anterior portion of GF. Posterior border of C4 reaches middle of GF.

Ac. Three pairs of Ac in two rows. Ac of equal size with no gaps between first, second and third Ac.

I-L-6. Claws with a series of clawlets in the two Indian species and in the African P. cooki; claws simple and hook-like in all other species.

IV-L-6. IV-L-6 more or less flattened, with partly serrated border and with rows or groups of setae out of which one terminal seta may be slightly enlarged. Variations in the setae and relative size of IV-L are one of the characters used to distinguish the species.

Palpus. Palpus "mamersopsid-like" in all presently known species of *Platymamersopsis* (s.s.), and palp untypical with swollen P4 and with claw at P5 large and unfused in *P.* (*Neomamersella*). Ventral seta on P2 strong and often the largest and strongest seta of the whole palp. In several species from Africa (including *P.* (*N.*) *tototaensis*) several long setae are found on the dorsal side of P2 and P3.

Chelicerae. The chelicera is of a typical and stable shape in all 11 species of *Platymamersopsis* (s.s.) and differs slightly from this shape in the subgenus *Neomamersella* (Fig. 51). The shape is similar to that of the chelicerae in Bandakiinae, but more elongated, with the dorsal elevation less prominent and more rounded. The cheliceral claw small but heavy in *Platymamersopsis* (s.s.) and slender in *P.* (*Neomamersella*).

Further remarks

Nymphs. Described in the original description (Viets 1914) and discussed by Cook (1966). With three dorsal plates.
Larva. Unknown.
Habitat. Reported from streams and rivers.
Distribution. Reported from Africa (10 spp.) and India (2 spp.) only.

Taxonomic placement

I tentatively suggest keeping the genus with the Anisitsiellinae until the larvae of *Platymamersopsis* is described. Only characters of the larvae will allow a firmly based decision on the question of whether the genus should be shifted to the Bandakiinae, to which it is related by adult morphology, especially the shape of the chelicerae, the organization of the coxae, and the complete dorsal and ventral shield. It differs from the Bandakiinae in the reduction of claws at IV-L and in the position of Cg4. However these character states could be derived (on the basis of the situation found in Bandakiinae).
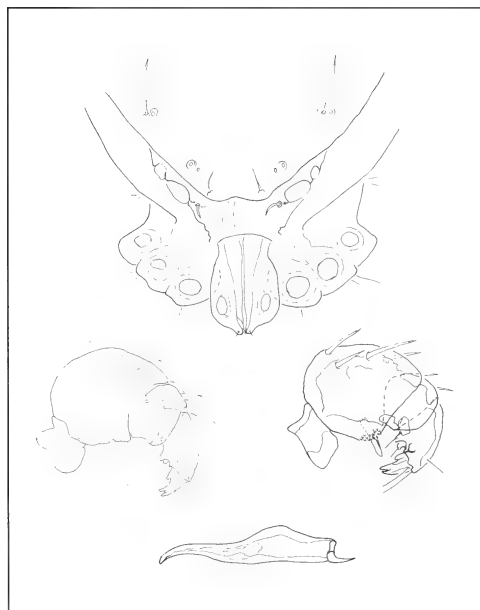
FIG. 52. *Paddelia eichhorniae* sp. nov. Top: frontal region of the idiosoma seen anteriodorsally. Middle: palpus in lateral (l) and medial (r) view. Bottom: chelicera.
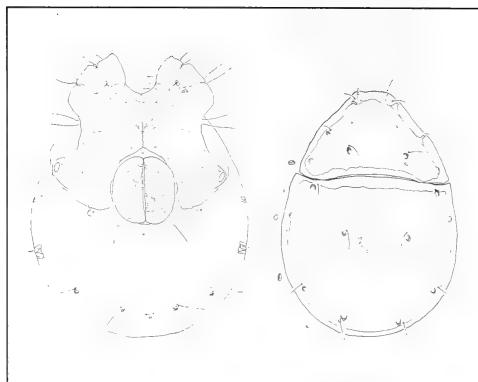
FIG. 53. *Paddelia eichhorniae* sp. nov. Left: ventral shield. Right: dorsal shield.

Genus: *Paddelia* gen. nov. [1 sp.]

Typus generis: *Paddelia eichhorniae* sp. nov.
Material examined: Type series.
Location of types: NMB, paratype will be deposited in ZSI

Definition (adults)

Characters of the Anisitsiellinae as defined above and:
- The Cg4 is situated at the tip of a finger-like protrusion on C2 near suture C2/C1 and just medially of the insertions of the second legs on the ventral side of the coxae.
- C1-C3 projecting well beyond the border of the idiosoma. Suture C1/C1 weak or only partly expressed.
- VS and DS complete; DS divided into anterior and posterior shield as in Fig. 53. Dorsal furrow narrow and without glandularia.
- Shape of chelicerae as in Fig. 52.

Species included

Paddelia eichhorniae sp. nov. discovered near New Delhi in stagnant ponds covered with lotus and water hyacinth (*Eichhornia crassipes*) is the only species of the genus.

Inventory (adults)

DS/VS. See definition.
Eyes. Eyes fused to ventral shield.
Coxae. See definition.
Cg4. See definition.
GF. C4 closely impending anterior two-thirds of GF. At level of second acetabula the genital opening ex-

tends slightly lateral to the genital flaps (similar to *Anisitsiella*). Posterior border of C4 reaches posterior border of GF.

Ac. Three pairs of Ac in two rows. Ac of equal size with no gaps between first, second and third Ac.

I-L-6. Claws with a series of ventral clawlets.

IV-L-6. IV-L-6 flattened to a paddle with 3–4 setae on the lateral side and serrate anterior and posterior margins.

Palpus. Palpus "mamersopsid-like." Ventral seta on P2 strong and pointed, surface medial to the insertion of this seta denticulate, P4 with two well-developed ventral protrusions.

Chelicerae. Similar to the chelicerae in *Platymamersopsis*, but dorsal elavation of the basal segment lower and more elongated.
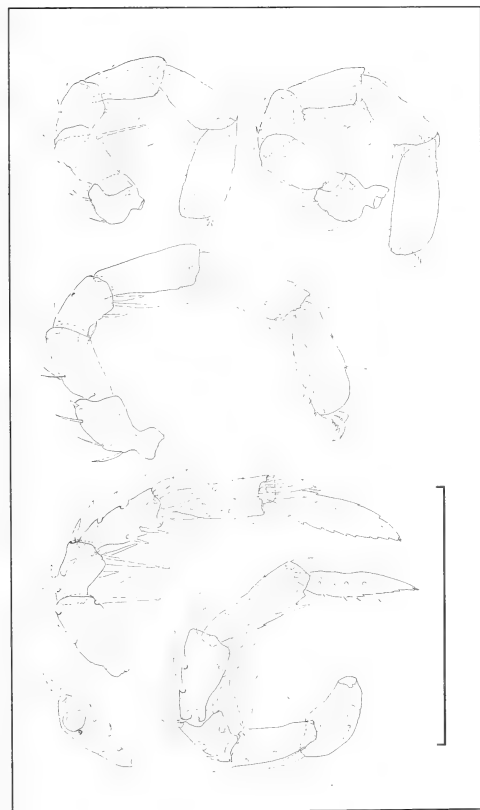
FIG. 54. *Paddelia eichhorniae* sp. nov.: I-L (top left), II-L (top right), III-L (middle), IV-L-2-6 in lateral view (bottom left), IV-L-1-6 in medial view (bottom right). Scale bar = 150 μm.

TABLE 26. *Paddelia eichhorniae* sp. nov. 1: Idiosoma [Measurements in μm].

Paddelia eichhorniae sp. nov. Collection 1990-09-26 "350" Specimen number: sex [m = male; f = female]	Holo-type (1) m	Allo-type (5) f
Idiosoma and Dorsal shields		
total length	387	392
total width	298	378
anterior dorsal shield: length	99	119
anterior dorsal shield: width	206	218
posterior dorsal shield: length	229	260
posterior dorsal shield: width	253	269
Coxae		
left to right width C3	396	206
left to right width insertions IV-L	240	276
left to right distance Cg4	99	96
Genital field (GF)		
genital opening: width	85	94
genital opening: length	90	108
genital flaps: length	94	108
genital opening: length/width ratio	1,06	1,15
Chelicera		
basal segment: length	105	105
basal segment: height	25	26
basal segment: length/height ratio	4,2	4,04
claw: length	21	20
claw: height	19	16
claw: length/height ratio	1,11	1,25
total length of chelicera	127	125

Taxonomic placement

Paddelia shares several characters with *Platymamersopsis*. The character clearly separating the genus from *Platymamersopsis* is the extremely flattened IV-L-6. Other differences include the position of Cg4, the shape of the chelicerae, and the dorsal shield (which is entire in *Platymamersopsis* and divided into two plates in *Paddelia*).

Paddelia eichhorniae sp. nov.

Holotype: 1 male adult from collection "1990-09-26 [-350-]" (pond near Hindon river, 500 m upstream of National Highway 24; 200 m a.s.l.; U.P., India). Paratypes: 2 males and 2 females with same data as holotype; coll. "1990-09-30 [-65-]" at locus typicus: 2 males, 1 female.
Type material placed in the NMB. A parataype will be deposited in the ZSI (India).

TABLE 27. *Paddelia eichhorniae* sp. nov. 2: Palpi [measurements in μm].

Paddelia eichhorniae sp. nov. Collection 1990-09-26 "350" Specimen number: sex [m = male; f = female]	Holotype (1) m	Allotype (5) f
Palpal segments		
P1-length	15	17
P1-height	23	25
P1-length/height ratio	0,65	0,68
P1: % of total length	11,28	12,10
P2-length	53	55
P2-height	44	40
P2-length/height ratio	1,20	1,38
P2: % of total length	39,85	39,01
P3-length	17	23
P3-height	25	25
P3-length/height ratio	0,68	0,92
P3: % of total length	12,78	16,31
P4-length	29	26
P4-height	17	19
P4-length/height ratio	1,71	1,37
P4: % of total length	21,80	18,44
P5-length	19	20
P5-height	10	12
P5-length/height ratio	1,9	1,67
P5:% of total length	14,2	14,18
Palpus: total length	133	141
length ratio P2/P4	1,83	2,11

Description of adults. As given in the generic description. No major differences between males and females. Measurements as given in Table 26 and Table 27. Measurements of legs (holotype 350, No 1) as:
Length of I-L-1 to I-L-6 = 40 / 58 / 41 / 56 / 61 / 81
Length of II-L-1 to II-L-6 = 46 / 55 / 45 / 61 / 77 / 81
Length of III-L-1 to III-L-6 = 54 / 55 / 46 / 73 / 79 / 83
Length of IV-L-1 to IV-L-6 = 61 / 58 / 40 / 60 / 73 / 86
Nymphs. Unknown.
Larva. Unknown.
Habitat. Discovered near a lowland river in stagnant ponds covered by plant carpets.
Distribution. Known from the locus typicus near New Delhi (India) only.
Derivatio nominis. The name for the genus refers to the paddle-like IV-L-6, the name given to the species refers to the water hyacinth (*Eichhornia crassipes*) which was abundant at the collection site.

Genus: *Gilatonia* K.O. Viets & Böttger, 1974 [1 sp.]

Genotype: *Gilatonia triscutata* K.O. Viets & Böttger, 1974
Material examined: Holotype, slide 4704, SMF
Location of types: SMF

Definition (adults)

Characters of the Anisitsiellinae as defined above and:
- DS in three parts, with one posterior and two anterolateral shields. The three shields are adpressed to each other and cover the whole dorsal surface.
- A suture separates off the small platelets on the median side from C3.
- IV-L-6 stocky, with claws reduced, and with 1 long terminal and +/– 10 subterminal setae (Fig. 56).

Species included

Gilatonia triscutata K.O. Viets & Böttger, 1974, reported from a stream in the Congo region (Zaire) with a single male specimen, is the only known species of the genus.
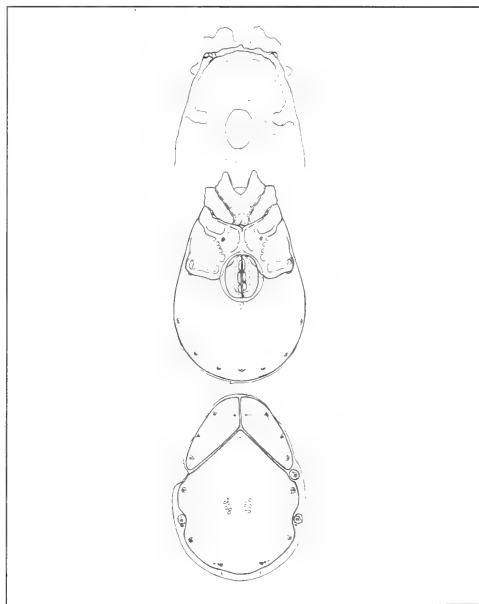
FIG. 55. *Gilatonia triscutata* K.O. Viets & Böttger, 1974. Top: dorsal view of ventral shield, anterior part with eye region and projecting coxae. Middle: ventral shield. Bottom: dorsal shield. [Top: original figure; middle and bottom figures from Viets *et al.* (1974)].
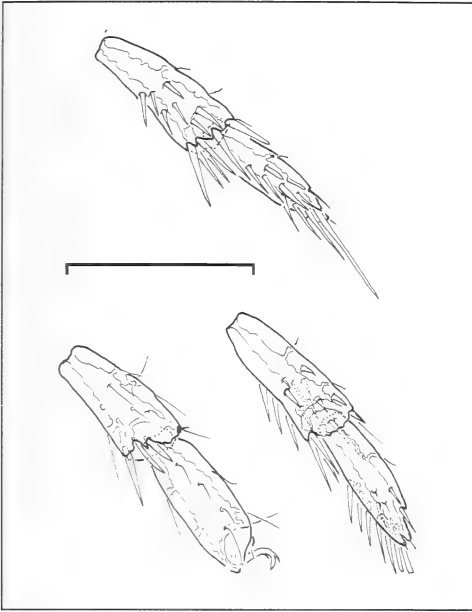
FIG. 56. *Gilatonia triscutata* K.O. Viets & Böttger, 1974 (holotype, male): Left IV-L-5,6 (top), right IV-L-5,6 (middle), I-L-5,6 (bottom). Scale bar = 100 μm.

Inventory (adults):

DS/VS. VS and DS complete. For arrangement of DS see definition.

Eyes. Eyes fused to the lateral edges of the ventral shield.

Coxae. First coxae fused medially, suture only weakly expressed. Anterior border of C3 concave. Similar to the situation in *Bandakia* and *Utaxatax*, a medial platelet appears to be separated from C3 by a suture parallel to the main axis of the body. However, in *Gilatonia* this platelet extends posteriorly and cuts off a small medial part of the fourth coxae as well.

Cg4. The Cg4 is situated medial to the suture C3-C4 (while in *Bandakia* and *Utaxatax* Cg4 is situated on the anterolateral edge of the median platelet).

GF. C4 closely impending anterior half of GF. Posterior border of C4 reaches middle of genital flaps.

Ac. Three pairs of Ac of equal size, no gap between first, second and third Ac.

I-L-6. I-L-6 with setae reduced to hairs and claws hook-like with a ventral and a dorsal clawlet.

IV-L-6. See definition; no swimming hairs present.

Palpus. Palpus of characteristic shape, with P4 and P5 slightly swollen. Figure depicted by Viets & Böttger

(1974, p. 124, Fig. 28) shows 5 dorsal setae situated in a row: 1 seta on P1, 3 on P2, and 1 on P4. There are no other lateral or ventral setae or hairs shown in Viets & Böttger (1974). The segment P5 is little less than one-third of P4 in length. It is specific in possessing 3 strong seta-like claws at its distal end, which are half as long as P5.

Chelicerae. In the holotype preparation the chelicerae are in the gnathosoma and both are seen from dorsal position only. Hence no information on the chelicerae is available, other than the total length which is approximately 115 μm.

The nymphs of *Mamersella thienemanni* show one posterior and two anterolateral platelets. However, the unsclerotized surface between them is large. *Nilotonia* adults and larvae, and a number of other genera, do possess a small posterior platelet, and in addition two even smaller anterolateral platelets, all of which are usually round or oval in shape.

Hydrobaumia malacensis is the only genus in which the adults show a similar arrangement of dorsal shields. Whereas in *Hydrobaumia* 6 rectangular platelets with one gland each surround the 3 anteromedial plates, in the case of *Gilatonia* 4 glands, with small round platelets, are situated laterally in the dorsal furrow.
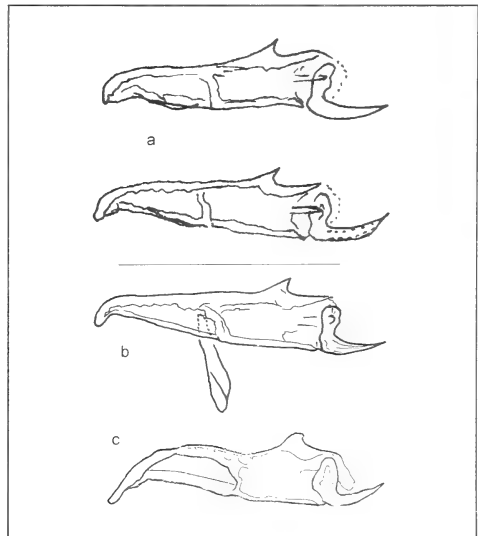
FIG. 57. *Mamersides* group: Typical shape of chelicera with an anterior-pointing edge at the dorsal border of the basal segment. (a) and (b) *Mamersides ruttneri*, (c) *Hydrobaumia malacensis* (Fig. b: unpublished figure by Halik, found in NHB).

Mamersides-group

Four of the five genera included in this group, *Hydro-baumia, Mamersides, Mamersopsides* and *Navamamer-sides*, are characterized by an anterior-pointing hook on the dorsal border of the basal cheliceral segment.

In the fifth genus, *Mamersopsis*, the state of this character is still undescribed. However it shares with two of the genera (*Hydrobaumia, Mamersopsides*) a characteristic dorsal sclerotization, composed of one or three shields covering a larger central area, which is surrounded by several +/− rectangular platelets. VS and DS are always complete.

Palpus "anisitsiellid-like" or "mamersopsid-like."

Genus: *Hydrobaumia* Halik, 1930 [1 sp.]

Typus generis: *Hydrobaumia malacensis* Halik, 1930.
Location of genotype: The holotype was not found in the NHB and is most probably lost; however some unpublished original drawings by Halik were discovered and are given below. No material examined for this study.

FIG. 59. *Hydrobaumia malacensis*: (a) gnathosoma and palpus (ventral view), (b) chelicera, (c) idiosoma (lateral view), (d) gnathosoma and palpus (lateral view), (e)–(h) legs 1–4.

Definition (adults)

Characters of the Anisitsiellinae as defined above and:
- Unique arrangement of dorsal shields in nine parts, with one large posterior and two anterolateral shields, surrounded by three pairs of +/− rectangular plate-lets.
- Dorsal furrow small, as are parts of the ventral shield seen from dorsally.

Species included

Hydrobaumia malacensis Halik, 1930 was reported with a single male from a rainforest brook near Batu Pahat in Johore (Malaysia). It is the only known species of the genus.

Inventory (adults; male only)

DS/VS. DS and VS complete. For arrangement of plates in the DS see definition.

FIG. 58. *Hydrobaumia malacensis* Halik, 1930: Pal-pus (top), dorsal shield (middle), ventral shield (bot-tom) [Figs. from Halik (1930)].

Eye-region. Eye-lenses and adjacent glands and plate-lets are all fused into the VS.

Coxae. Suture C3/C4 incomplete and bent anteriorly (compare nymphal stages of *Bandakia* or *Utaxatax*).

Cg4. Cg4 not mentioned in the text of Halik (1930). The form of C3 and C4 suggests that it is situated near to the suture C2/C3 (similar to the situation in *Bandakia* or other genera, where it is found at the tip of a finger-like protrusion arising from C4).

GF. Not closely impended by C4. With first or second pair of Ac at level of insertions of C4.

Ac. Ac elongated, in two rows formed by three pairs, without gaps between the Ac of a row.

I-L-6. I-L-6 with setae reduced to hairs and claws with ventral clawlet.

IV-L-6. With serrate border and two small setae, and without well-developed claws.

Palpus. Ventral tubercle on P4 small, but clearly visible. Ventral seta of P2 short and thick. Distribution of setae on lateral side and measurements acc. to Fig. 3 in Halik (1930) are: P1 with no seta; P2 with 4 dorsal and 1strong ventral setae; P3 with 2 lateral setae; P4 with no seta and 1 dorsodistal hair; P5 without seta and with 3–4 minute claws.

Chelicerae. According to Halik (1930), the chelicera is similar to that of *Mamersides*. An unpublished figure of the chelicerae (drawn by Halik, but not included in his publication) is given below. Total length of chelicerae is 212 μm.

Discussion of taxonomic placement

The DS arrangement is unique in *Hydrobaumia* (see definition). The only genus with a similar arrangement is *Mamersopsis*. In *Mamersopsis*, anterior to the largest dorsal shield, we find the pair of shields plus an additional medial shield protruding up to the anterior border of the body, and also two rows of six lateral plate-lets on each side with one, two or no glands, instead of the three pairs of lateral platelets with one gland each as in *Hydrobaumia*.

In *Hydrobaumia*, as in *Nilotonia* and *Gilatonia*, there is a larger posterior shield with a pair of shields anterior to it. In *Bandakia*, *Utaxatax* and *Mamersella*, these three shields are fused to the so-called "complete" dorsal shield in the adults, but are visible in the nymphal stage of *Mamersella*. The glands which surround this inner area, are (1) without platelets (e.g *Nilotonia*), (2) with small platelets (e.g., some *Bandakia*-species), or (3) with +/– rectangular platelets which fill out most of the space of the dorsal furrow (some *Bandakia* species, *Stygomamersopsis*, *Psammo-*

torrenticola). In some species additional platelets are found next to platelets with glands. Rarely, as in *Mamersopsis*, two glands are fused to one common lateral platelet. The number and position of these platelets surrounding the central area, and the number of platelets fused to the central area, differs from species to species, and at the species level between male and female and nymph and adults. In *Bharatonia vietsi* and *Shivatonia acetabulensis*, the two anterior shields of *Hydrobaumia* are fused to a single anterior shield, and the central area is divided into an anterior and a posterior shield. In the females and nymphs of these two species not a single gland is fused to the two central shields, while in the males two pairs of glands are fused to the posterior shield. The diversity in secondary sclerotization is of little help in higher systematics. I suggest placing *Hydrobaumia* next to *Mamersopsis* for the shared character state "chelicerae with small and anteriorly-pointing hook on the dorsal surface of the basal segment" mentioned in the text of Halik (1930) and depicted in the drawing published here found in the NHB.

Genus: *Mamersides* Viets, 1935 [2 spp.]

Typus generis: *Mamersides sarangensis* Viets, 1935. Material examined: *Mamersides sarangensis* paratype, slide 7687, SMF; *Mamersides ruttneri* paratype, slide 7707, SMF ; *Mamersides ruttneri* [coll. Landberg], material from SMH. Location of t.g.: SMF

Definition (adults)

Characters of the Anisitsiellinae as defined above and:
- DS and VS complete.
- Medial borders of C4 +/– straight, touching but not surrounding genital field. Posterior border of right and left C4 are together form a zigzag line between the insertions of fourth legs. Lateral and medial parts of the posterior border of C4 as well the two medial borders are positioned +/– rectangular to each other.
- A waved lateral border starts anterior of the insertions of IV-L and reaches the anterior border of the body.
- No swimming hairs present on IV-L-4,5,6. Instead there may be a series of feathered medium-long setae and few long or medium-long spatulate, feathered setae.
- C3/C4 incomplete or C3/C4 turning anteriorly when one quarter of the total distance between lateral border C3 and medial border C4 still remains.
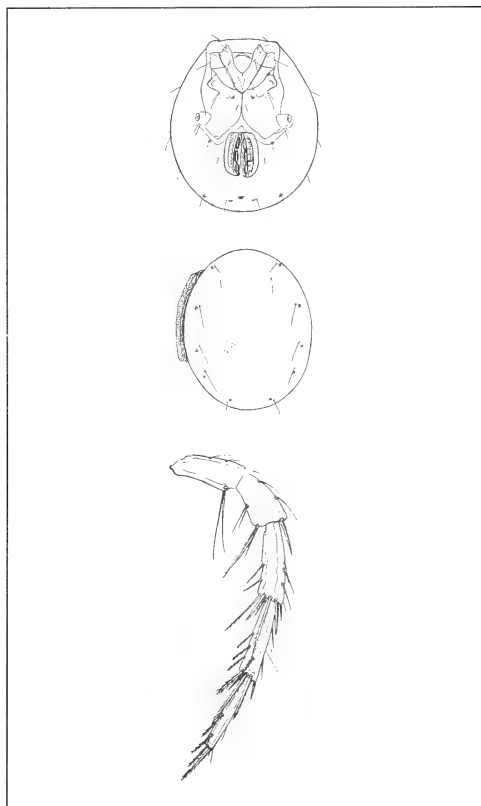- Cg4 on the level of the posterior border of C3, medial to suture C3/C4.

FIG. 60. *Mamersides sarangensis* Viets, 1935 (female): Ventral shield (top), dorsal shield (middle), IV-L-2-6 (bottom) [Figs from Viets (1935)].

C3 slightly smaller or same as this distance in C2 (slightly larger in females of *M. ruttneri* only). Consequently insertions of III-L are situated posterior and not lateral to insertions of II-L.

Cg4. See definition.

GF. GF in the posterior half of the body. The relative and absolute size of the GF is in males much smaller than in females.

Ac. Three pairs of Ac of equal size. Without or with small gaps between first, second and third pair of Ac.

I-L-6. Claws simple, hook-like with a small ventral hair (confirmed for *M. ruttneri* only).

IV-L-6. Insertions of IV-L well anterior to the anterior border of the genital field. Chaetotaxy of IV-L-2-6 in *Mamersides sarangensis* as given in Fig. 60.

Palpus. Palpus of the „anisitsiellid-type." Ventral seta of P2 shorter than ventral border of P2. Ventral tubercles on P4 small. Setae, hairs and measurements (with d.l. = Dorsal length; h=hight) as given for *M. sarangensis* in Viets (1935) are: P1 with 1 dorsal seta and d.l. of 21 µm; P2 with 3–4 dorsal setae, 1 short ventral seta, a d.l. of 74 µm; and a hight of 56 µm; P3 with 2–3 setae, a d.l. of 41 µm, and a hight of 29 µm; P4 without seta, 1 dorsodistal hair, 3 ventral hairs, a d.l. of 112 µm and a hight of 22 µm; P5 without seta, 1–2 hairs; 3–4 small claws, and d.l. of 21 µm.

Chelicerae. 100 µm total length; 74 µm basal segment and 46 µm claw (in *M. sarangensis*). Dorsal border of basal segment of typical shape, with sharp anterior-pointing hook. Shape of chelicera very similar in the two species included in the genus.

Species included

Mamersides sarangensis Viets, 1935 and *Mamersides ruttneri* Viets, 1935, both reported in both sexes from springs in Java, Indonesia (Asia), are the only know species of the genus. Lundblad (1971) confirms the presence of *M. ruttneri* in springs in eastern and central parts of Java, and gives additional information incl. figures of the chelicerae, gnathosoma and some photographs of his slides. Nymphs and larvae are unknown.

Inventory (adults)

DS/VS. DS complete, with six pairs of glandularia. VS complete.

Eye-region. Eye-lenses on anterolateral edges of ventral shield.

Coxae. Maximum distance between lateral borders of

FIG. 61. *Mamersides ruttneri* Viets, 1935: Chelicera from coll. Landberg; Java, Pagilaran. 20.1.1939; SMH (top); chelicera of paratype [slide 7707 in SMF] (bottom).

Genus: *Mamersopsides* Viets, 1916 [2 spp.]

Genotype: *Mamersopsides sigthori* Viets, 1916. Location of genotype: lost (not found in SMF). No material examined for this study.

Definition (adults)

Characters of the Anisitsiellinae as defined above and:

- C4 with sharply pointed posterior end. Medially from this posterior tip, C4 closely impends at least the anterior half of GF and laterally from this point the edge leads straight towards the more anteriorly placed insertions of IV-L. A suture leads from insertion of IV-L to the insertions of III-L.
- DS complete, oval and with a well-developed ridge on each side near the lateral margins.
- Dorsal furrow with 5–7 pairs of medium-sized and +/− rectangular platelets. Sometimes two glands in the dorsal furrow are fused to a common platelet.

Species included

Mamersopsides sigthori Viets, 1916, was reported with a single male only from a stream near the street Bonapupa-Lungasi in Cameroon (Africa). *Mamersopsides vietsi* Cook, 1966 was the second species discovered, with male and female, in a stream one mile north of Suehn (Liberia, Africa).

Inventory (adults)

DS/VS. For DS see definition. VS complete, including excretory pore. Two pairs of glands lateral to the excretory pore are presents in the VS in the male *M. sigthori* and in the female *M. vietsi*, but in the dorsal furrow the male of the latter species.

Eye-region. Eye-lenses appear to be located in the anterolateral corners of the nasale, according to figures in Cook (1966), but no information is given in the text.

Coxae. Coxal organization: posterior borders of C2 convex; medial sutures of C1/C1, C3/C3 and C4/C4 forming a straight line between GF and gnathosoma, with medial suture of C1/C1 present or incomplete due to fusion.

Cg4. Cg4 situated posterior to suture C2/C3 in semilateral position.

GF. Anterior end of GF level with or posterior to insertions of IV-L.

Ac. Acetabula ein two straight rows of three pairs without gaps between them and with third pair smaller and roundish.

I-L-6. No information on claws in Cook (1966).

IV-L-6. Without claws and without swimming hairs. No leg depicted. *M. sigthori* with terminal elongated seta (not depicted).

Chelicerae. Most probably with "*Mamersides*-like" chelicerae in *M. sigthori*, as Viets (1916) notes: "Es fehlt nicht eine vorspringende Ecke an der Dorsalseite ihres Grundgliedes" (= sharp tooth on dorsal border of basal segment not missing). However, this tooth seems to be hidden by the border of the gnathosoma in the figure given by Viets (1916, plate 2, fig. 5d). Cook (1966) gives the total length of the chelicerae (female 173 µm, male 176 µm) in *M. vietsi* without any further comment on its shape.

Palpus. Palp of the "anisitsiellid-type." P1 with dorsal seta. Ventral seta of P2 shorter than ventral border of P2. Ventral tubercle on P4 small. Denticles on tip of P5 small. A very similar shape and an identical chaetotaxy is found in the palp of both the included species. Cook (1966) gives data for dorsal lengths (= d.l. male/female) of palpal segments in *M. vietsi*: P1 with d.l. 21/19 µm and 1 dorsal seta. P2 with d.l. 80/79 µm, with 3–4 dorsal and with 1 ventral seta. P3 with d.l. 42/42 µm and with 2 lateral, and 2 medial setae. P4 with d.l. 81/80 µm without seta, with 1 dorsodistal hair, and with 4 ventral H on small hooks. P5 with d.l. 25/24 µm, without seta, with 1 hair, and with 3–4 minute claws.

FIG. 62. *Mamersopsides sigthori*: Palpus (top), ventral shield (bottom left), dorsal shield (bottom right) [Figs. from Viets (1916)].

Discussion of species, locations of holotypes

Mamersopsides vietsi Cook, 1966 differs from *Mamersopsides sigthori* Viets, 1916 in the proportionally much longer and narrower fourth coxae of the latter. Figures of *M. vietsi* are given by Cook (1974); figures of the VS, DS and palp of *M. sigthori* Viets, 1916 are given below. Holotype of *M. sigthori* most probably lost (not found in SMF). Types of *M. vietsi* in CNM.

Taxonomic placement

Mamersopsides appears to be most closely related to *Mamersides*, on the basis of the similar shape of the chelicerae and several other features (e.g., chaetotaxi and shape of palp; suture leading anteriorly from insertions of IV-L; insertions of IV-L without condyles; C4 forming a long medial suture with each other). Nymphs and larvae of both species are unknown.

Genus: *Mamersopsis* Nordenskiöld, 1905 [3 spp.]

Typus generis (t.g.): *Mamersopsis thoracica* Nordenskiöld, 1905. Location of t.g.: unknown. No material examined for this study

Definition (adults)

Characters of the Anisitsiellinae as defined above and:
• VS complete and DS divided into a larger posteromedian plate and several anterior and lateral platelets as given in Fig. 63.

Species included

Mamersopsis thoracica Nordenskiöld, 1905 is based on 4 specimens from the White Nile (backwaters north of Kaka and among water plants north of Gebel). *Mamersopsis thoracica* and *Mamersopsis circumclusa* Viets, 1994 were both described from Africa, while the single female of *Mamersopsis viridis* Viets, 1935 was reported from wet rice fields in Sumatra (Indonesia).

Inventory (adults)

DS/VS. See definition.
Eye-region. Anterior eye-lenses in anterolateral edges of ventral shield. Posterior eye-lenses fused to the separate small platelets forming the anterolateral edges of the dorsal shield.
Coxae. A well-developed ridge leads straight anteriorly from the insertions of IV-L.
Cg4. Not described. However the shape of C3 and C4 suggest that it is situated near to the suture C2/C3,
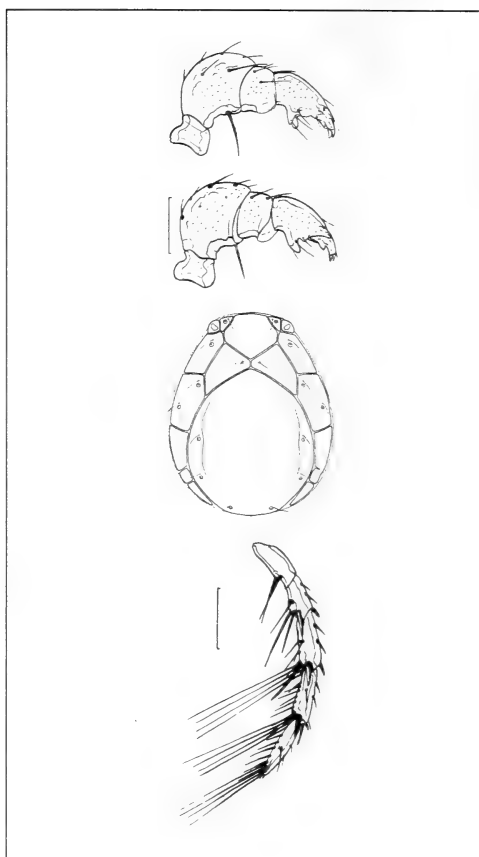
FIG. 63. *Mamersopsis viridis* Viets, 1935 (female): Palpi (top) [scale bar = 50 µm]; dorsal shield (middle), IV-L-2-6 (bottom) [scale bar = 100 µm]. Figs. from Viets (1935) and Cook (1974), middle.

similar to the situation in several other related taxa, where it is found in the anterolateral edge of a protruding portion arising from C4.
GF. C4 closely impends the GF. C4 projects posterior to GF in *M. circumclusa* reaches the posterior end of the GF in *M. thoracica*, and ends anterior to the posterior end of the GF in *M. viridis*. Insertions of C4 at level of GF.
Ac. Three pairs of small Ac of equal size. With small gaps between first, second and third pairs of Ac.
I-L-6. Claws simple, hook-like.
IV-L-6. Chaetotaxy of IV-L-2-6 in *M. viridis* as given in Fig. 63; *M. circumclusa* very similar; *M. thoracica* not adequately described, but with a "few swimming hairs present."

Palpus. Palpus of the "mamersopsid-type."

Chelicerae. Not described in *M. thoracica*. Shape of dorsal border of basal segment not visible in the figures of the gnathosoma of *M. viridis* and *M. circumclusa*. Total length of chelicera in *M. viridis* approx. 165 μm. Shape of claw similar to *Platymamersopsis*.

Taxonomic placement

Dorsal shield rather similar to that of *Hydrobaumia* but without the unpaired anterior shield of the latter. Ridge leading anteriorly from insertions of IV-L similar to *Mamersides*. Shape of chelicera uncertain, similar to *Platymamersopsis* or to *Mamersides*. Larvae and nymphs unknown.
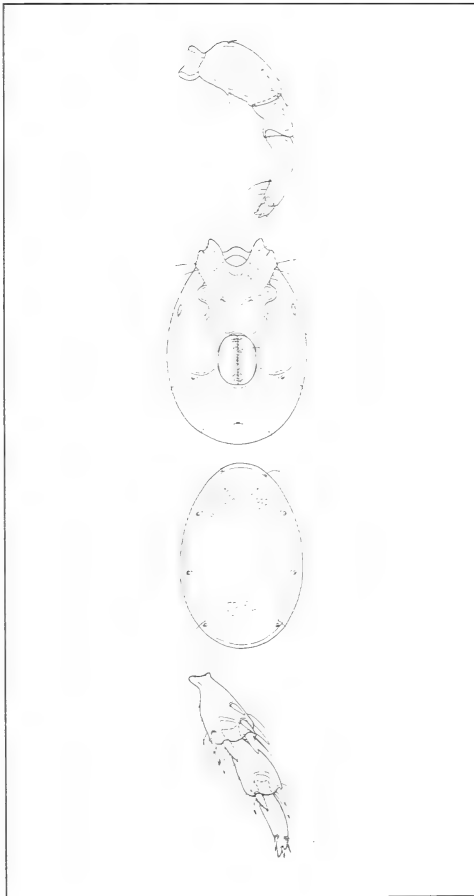
FIG. 64. *Navamamersides karekari* Cook, 1967: Palpus (top), ventral and dorsal shield (middle), IV-L-4,5,6 (bottom). Figs. from Cook (1967).

Genus: *Navamamersides* Cook, 1967 [2 sp.]

Typus generis: *Navamamersides karekari* Cook, 1967. Location of type: CNM (?). No material examined for this study.

Definition (adults)

Characters of the Anisitsiellinae as defined above and:
- Maximum distance between lateral borders of C3 clearly shorter than between lateral borders of C2. Insertions of IV-L displaced anteriorly, and much closer to the insertions of the III-L than to the posterior border of C4.
- IV-L-4,5,6 short, stocky and flattened, without well-developed claws.

Species included

Navamamersides karekari Cook, 1967, reported with both sexes from seepage areas in Maharashtra state and Kerala state (southern India) is the type-specimen of the genus. As a second species, a single female of *Navamamersides similis* Cook, 1967 was discovered in a small stream in Kerala state (southern India).

Inventory (adults)

DS/VS. DS and VS complete. DS with four glandularia and a well-developed peripherally-located ridge, except at anterior end.

Eye-region. No information given by Cook (1967).

Coxae. See definition. C1 and C2 extending anterior to the border of the body proper. Gnathosoma bay gradually widening anteriorly. Coxae in region of insertions of III-L rounded. Suture C3/C4 complete and extending in an almost posterior direction. Posterior border of C4 round.

Cg4. The Cg4 is situated anteriorly on C3, near midlength of suture C2/C3.

GF. C4 closely impending GF. Posterior border of GF slightly posterior to posterior border of C4.

Ac. Three pairs of elongated Ac; no gaps between first, second and third pair.

I-L-6. With setae reduced to 3–6 hairs and claws hook-like.

IV-L-6. See definition.

Palpus. Palp of the „anisitsiellid-type." Ventral seta of P2 very short and surface distally of this seta rippled. Ventral tubercle on P4 small. Data from Cook (1967) for 5 females of *N. karekari* are given in the following: P1 without seta and with dorsal length (d.l.) 26–28 μm. P2 with 3 dorsal and 1 short ventral setae, and with d.l. 111–114 μm. P3 with 2 setae and with d.l. 48–55 μm. P4 without seta, with 1 dorsodistal and

3 ventral hairs, and with d.l. 89–90 μm. P5 without seta, with 1 hair and 3 small claws, and with d.l. 22–24 μm.

Chelicerae. Total length of chelicerae reaches 173 μm in females and 149 μm in males of *N. karekari* and 149 μm in the female of *N. similis.* Dorsal side of the basal cheliceral segment with a well-developed pointed projection.

Taxonomic placement

Cook (1967) suggests that *Navamamersides* is most closely related to *Mamersides.* However, he gives no information on the shape of the chelicerae other than "dorsal side … with a well-developed pointed projection." This could refer to the situation in *Mamersides* as well as in Bandakiinae. The organization of the coxae, with insertions of IV-L displaced anteriorly, is intermediate between the character state as expressed in *Bandakia* and *Utaxatax.* The stocky IV-L is also found in *Utaxatax gereckei* sp. nov.. Hence the genus could also be related to the Bandakiinae. Until information on the chelicerae is available it is tentatively assigned to the *Mamersides*-group of the Anisitsiellinae.

Mahemamersides-group

The two genera in this group, *Nilgiriopsis* and *Mahemamersides,* have a IV-L-6 with extremely serrate margins with the cross-section of this segment +/− rectangular.

Genus: *Mahemamersides* Bader, 1985 [1 sp.]

Typus generis: *Mahemamersides boveyi* Bader, 1985. Material examined: Type series in NMB. Location of types: NMB.

Definition (adults)

Characters of the Anisitsiellinae as defined above and:
- I-L-6 possess claws with small ventral blade and ventral and dorsal clawlets.
- IV-L-6 flattened, with three highly serrate margins; a row of 4 small setae on its inner side and 3 small setae on the outer side; claws reduced to minute setae.
- C4 with a unique shape and with a well-developed ridge connecting the insertions of IV-L with the insertions of III-L.

Species included

Mahemamersides boveyi Bader 1985, discovered with both sexes in a forest spring at 400 m a.s.l. on Mahé in the Seychelles archipelago is the only known species of the genus.
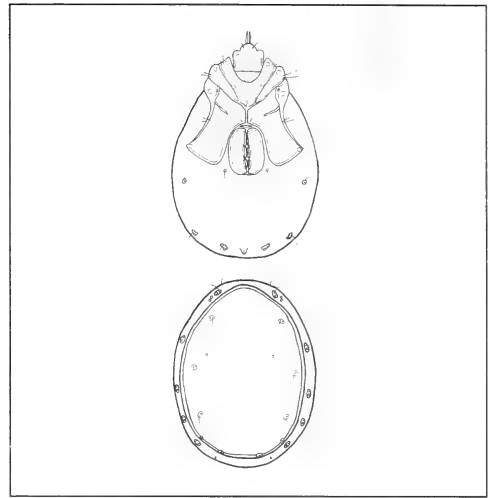
FIG. 65. *Mahemamersides boveyi* Bader, 1985: Ventral view (top), dorsal view (bottom). Figs. from Bader (1985).

Inventory (adults)

DS/VS. DS and VS complete.
Eye-region. Eye-lenses free in dorsal furrow.
Coxae. See definition. C1/C1 fused medially with suture incomplete; suture C3/C4 incomplete.
Cg4. Bader (1985) Cg4 identifies a glandularium posterior to C4 as Cg4 (Bader 1985, page 17, Fig. 2). However the incomplete suture C3/C4 suggests that Cg4 is situated on C3, as in most other related taxa.
GF. C4 closely impending GF in its anterior half, then slowly retreating. Posteromedial edge of C4 curved, posterolateral edge pointed. Posterior border of C4 slightly anterior to posterior border of GF.
Ac. Three pairs of elongated Ac; no gaps between first, second and third Ac. Length of Ac 31 μm.
I-L-6. See definition. With setae reduced.
IV-L-6. See definition.
Palpus. Palp "anisitsiellid-like." Ventral seta of P2 longer than ventral length of P2. Ventral tubercle on P4 small. The following data on palpus characters, including dorsal length (= d.l. male/female) are given in Bader (1985): P1 without seta, d.l. 15/19 μm. P2 with 7 dorsal setae, 1 ventrolateral seata and d.l. 74/83 μm. P3 with 2 dorsal and 1 lateral seta, and with d.l. 34/34 μm. P4 without seta, with 3 ventral hairs, and with d.l. 80/83 μm. P5 without seta, with 2 hairs, with 3 small claws, and with d.l. 22/25 μm.
Chelicerae. Total length of chelicerae 222 μm (fide Bader 1985).
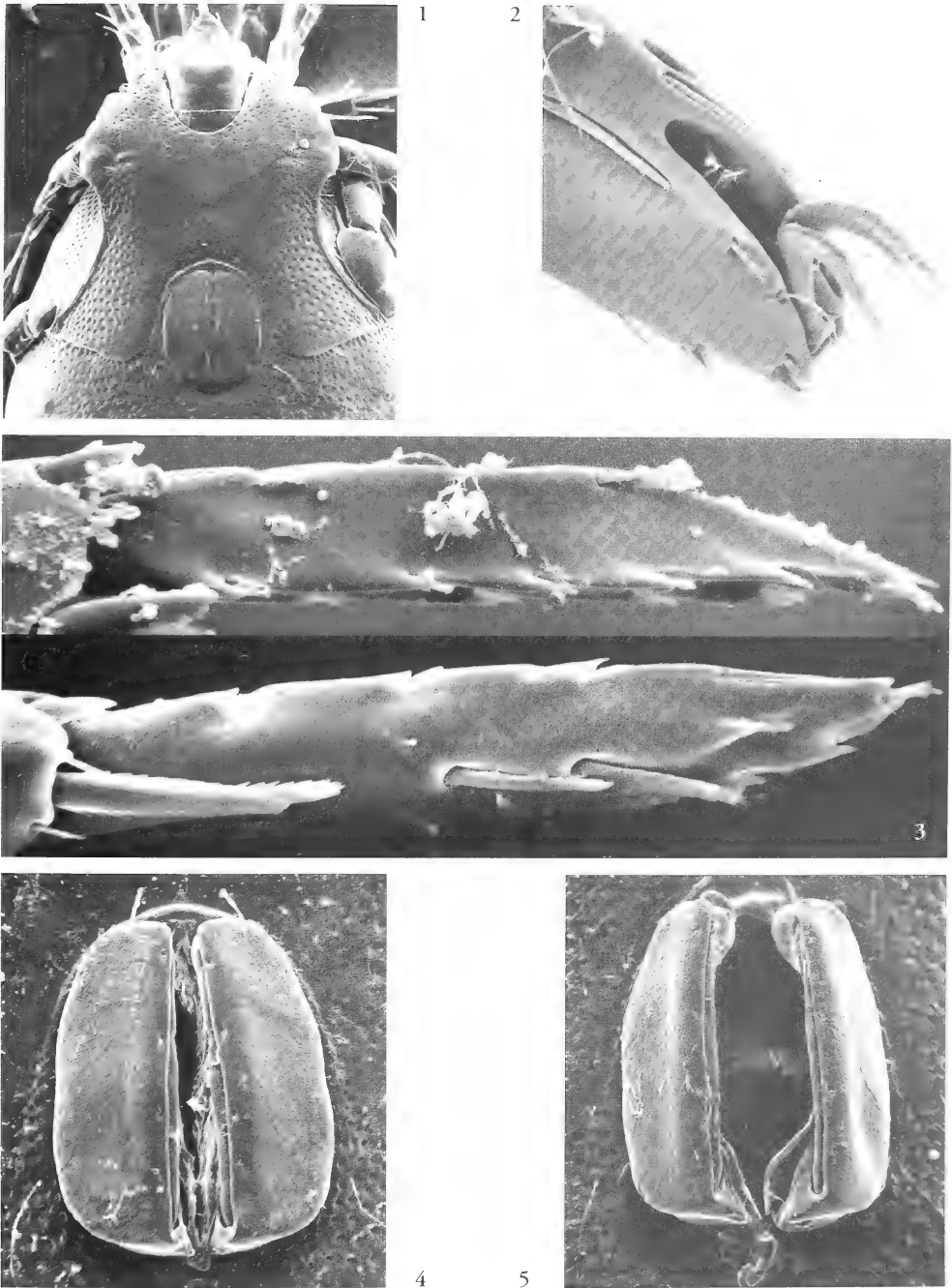
FIG. 66. *Mahemamersides boveyi* Bader, 1985: (1) Ventral shield, anterior part (male) [similar to Bader (1985), p 20, Fig. 3b], (2) Tip of III-L-6 with claw (female) [similar to Bader (1985), p 20, Fig. 3m], (3) IV-L-6 in two views (male), (4) Female genital field; flaps closed [similar to Bader (1985), p 20, Fig. 3m], (5) Female genital field; flaps open.

Taxonomic placement and further notes

Bader (1985) calls the ridge or elevation connecting insertions of IV-L and III-L unique. It is, however, similar to structures in several other genera (e.g., *Mamersopsides, Paddelia, Nilgiriopsis, Platymamersopsis, Shivatonia, Bharatonia*) and several species of *Nilotonia*.

The IV-L-6, with three highly serrate margins, is similar to that on the IV-L-6 of *Niligiriopsis*.

Unpublished REM photographs of *Mahemamersides* produced for the late Bader were found in the collection of the NHB. Some of them are shown here to give additional information on *Mahemamersides boveyi*.

Genus: *Nilgiriopsis* Cook, 1967 [1 sp.]

Typus generis: *Nilgiriopsis imamurai* Cook, 1967. Location of type: CNM (?). No material examined for this study

Definition (adults)

Characters of the Anisitsiellinae as defined above and:
- C1 - C3 projecting far anterior to the border of the body proper and C1 with anteromedial edge sharply pointed.
- Anterior end of DS pointed and flanked with a pair of glandularia, lying free in the integument. DS bearing five pairs of glandularia and a well-developed ridge.
- IV-L-6 without claws, flattened and with clearly serrate borders.

Species included

Nilgiriopsis imamurai Cook, 1967, reported with a single male specimen from a stream in southern India (two miles west of Vayitri, Kerala state, India), is the only known species of the genus.

Inventory (adult; male only)

DS/VS. VS and DS complete. For DS see definition.
Eye-region. No information given by Cook (1967).
Coxae. See definition. Suture C3/C4 incomplete. Posterior border of C4 round. Anterior border of C3 concave and medial suture formed by C3/C3 and C4/C4 nearly as long as GF.
Cg4. Cg4 on C3 near suture C2/C3, in the same position as in most *Bandakia* (but there is no suture present which would separate off a medial portion of C3).
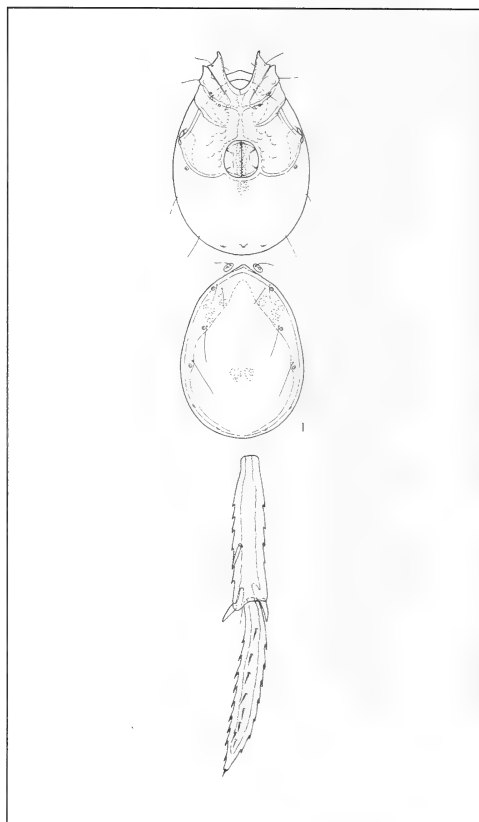
FIG. 67. *Nilgiriopsis imamurai* Cook, 1967: Ventral shield (top), dorsal shield (middle), IV-L-5,6 (bottom). Figs. from Cook (1967).

GF. C4 closely impending GF. Posterior border of GF at same level as posterior border of C4.
Ac. Three pairs of Ac of equal size. No gaps between first, second and third Ac.
I-L-6. With a few hairs and a few small setae. Claws hook-like.
IV-L-6. See definition.
Palpus. Palp of the „anisitsiellid-type." Ventral seta of P2 not longer than ventral border of P2. Ventral tubercle on P4 small: P1 with 1 seta. P2 with 3 dorsal setae and 1 medium ventral seta. P3 with 1 seta. P4 without seta, with 1 dorsodistal hair, and 4 ventral hairs. P5 without seta, with 1 hair, and with 3–4 terminal small denticles.
Chelicerae. Chelicerae with strong claw and cheliceral basal segment without dorsal elevation. Total length 186 μm.

Taxonomic placement

Placed here next to *Mahemamersides* because of the IV-L-6 with 3 highly serrate margins.

Anisitsiellides-group

The *Anisitsiellides*-group includes the three genera *Anisitsiellides*, *Zelandatonia* and *Sigthoriella*. Members of the group are found in Australia, New Zealand and South America. The genus *Sigthoriella* is only tentatively assigned to the genera-group (with reference to the shape of the chelicera). The taxonomic placement is discussed more extensively under the respective genera.

Genus: *Anisitsiellides* Lundblad, 1941 [11 spp.]

Typus generis: *Anisitsiellides monticolus* Lundblad, 1941. Location of t.g.: SMH. Material examined: *Anisitsiellides monticolus* holotype slide 3036, SMH.

Definition (adults)

Characters of the Anisitsiellinae as defined above and:
- IV-L with claws reduced to small spines; IV-L-5 distally with 1–3 long swimming hairs; claw at I-L-6 with ventral blade and clawlet
- Coxal organization with sutures C3/C3 and C4/C4 medially present and GF with anterior border clearly posterior to insertions of IV-L
- Cg4 just posterior to suture C3/C2 [2 spp.] or on C2 [9 spp.]
- Chelicerae with typical dorsal elevation in the proximal portion of the basal segment (but not so in *A. tabberabbera*)
- P4 either with strong ventral tubercles [5 spp.] or with ventral tubercles small [1 sp.] or absent [5 spp.]

Inventory (adults)

DS/VS. DS/VS complete.
Eyes. Lateral eyes fused to platelets which cut off an anterior portion of the ventral shield; these platelets are (1) separated medially [1 sp.], (2) fused medially [6 spp.], or (3) fused to the ventral shield [4 spp.].
Coxae. See definition and Fig. 69. Sutures C3/C2 (and sometimes C2/C1) medially reduced. C4 with posterior suture reduced (completely fused with ventral shield).
GF. Anterior border of GF posterior to level of insertions of IV-L.
Ac. Three pairs Acetabula without large gaps between them.

I-L-6. I-L-6 in most species with setae reduced to hairs.
IV-L-6. See definition and Fig. 71. Insertions of IV-L with condyles.
Palpus. Palpus variable (Fig. 70) from more or less "anisitsiellid-like" to "mamersopsid-like." P2 with ventral seta present, but reduced, not shown in the figure or lost in *A. tabberabbera* and *A. partitus*. P3 with several dorsal setae and one ventrolateral distal seta. P4 either with strong ventral tubercles [5 spp.] or with tubercles small [1 sp.] or absent [5 spp.]. P5 with claws small and fused.
Chelicerae. With characteristic dorsal elevation in the proximal part of the basal segment (Fig. 70), but this elevation not shown in the figure of *A. tabberabbera* (Harvey 1990, p. 644, Fig. 46).
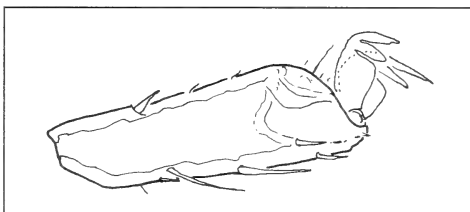
FIG. 68. *Anisitsiellides monticolus* (holotype). In *Anisitsiellides* the claws of the first three pairs of legs are equipped with a ventral blade and clawlet.

Further remarks

No information on nymphs and larvae is available.
Habitat. Known from creeks, streams and rivers. One species found in mosses and one in the hyporheic interstitial.

Species included

The following list gives the species included in the genus *Anisitsiellides*, the sex of the known specimens, the type locations and some information on the habitat. All species are known from few specimens and one sex only, and were usually discovered during a single collection.
(1) The female of *A. monticolus* Lundblad, 1941 is known from a stream at 3450 m a.s.l. near Paramo de San Rafael, Puracé, Columbia.
(2) the male of *A. lundbladi* Cook, 1980 is known from mosses on rocks on the bottom of a stream (Rio Negro), km 27 on road Bariloche-Tronador, Argentina.
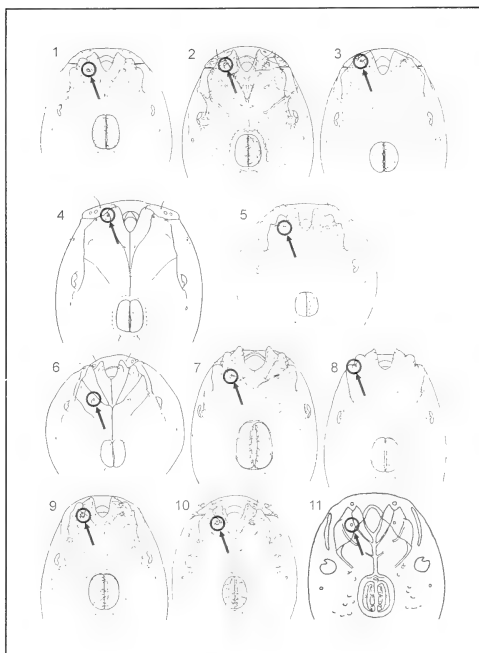
FIG. 69. Position of Cg4 in *Anisitsiellides*: (1) A. *mon-ticolus*, (2) A. *lundbladi*, (3) A. *chilensis*, (4) A. *caledonia*, (5) A. *circularis*, (6) A. *tabberabbera*, (7) A. *tolarda*, (8) A. *tasmanicus*, (9) A. *arraphus*, (10) A. *partitus*, (11) A. *zelandicus* [Fig. 1 from Cook (1988), other Figs. from original descriptions as given under "Species included"].

(3) The male of A. *chilensis* Cook, 1988 is known from a small stream in the El Purgatoria area of Las Trancas (near Recinto), Nuble Prov., Chile.
(4) The female of A. *caledonia* Harvey, 1990 is known from Caledonia River, Gippsland Regional Env. Survey site Mc6, Victoria, Australia.
(5) The male of A. *circularis* Cook, 1986 is known from Deer Park River between Dorrigo and Ebor, New South Wales, Australia.
(6) The female of A. *tabberabbera* Harvey, 1990 is known from Wentworth River, upstream of Tabberabbera, Victoria, Australia; 37°34′S, 147°22′E.
(7) The female of A. *tolarda* (Cook, 1986) is known from a hole dug in gravel bar in the Little Florentine River on Gordon River Road (west of Maydena), Tasmania, Australia.
(8) The male of A. *tasmanica* Cook, 1986 is known from the Little Florentine River on Gordon River Road (west of Maydena), Tasmania, Australia.

(9) The female of A. *arraphus* Cook, 1983 is known from from Te Whaiau Stream at junction of Rt. 47 and Rotaria Road, North Island, New Zealand.
(10) The female of A. *partitus* Cook, 1983 is known from Whale Creek on Rt. 6, west of Murchison, South Island, New Zealand.
(11) The female of A. *zelandicus* Hopkins, 1967 is known from a small, gravel-bedded tributary of the Mangatarere River, Tararua Mountains, New Zealand.

Taxonomic placement

The position of the genus *Anisitsiellides* will remain uncertain until information on nymphs and larvae can be provided. However it is placed in this study under
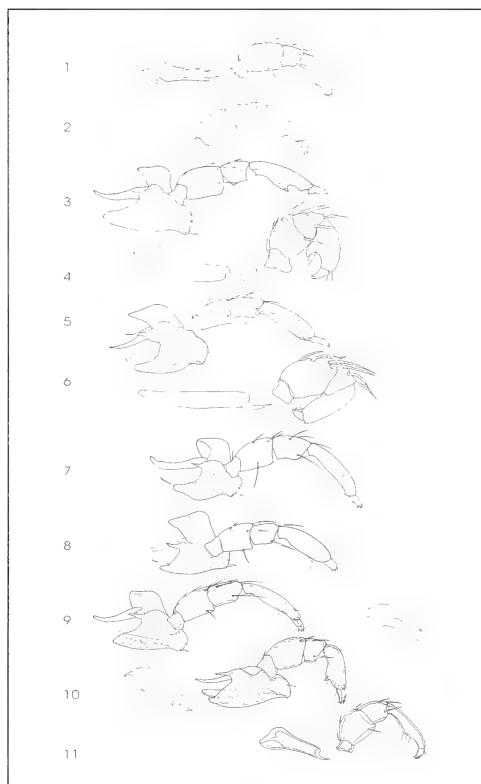
FIG. 70. Shape of palpi, chelicera and gnathosoma in *Anisitsiellides*: (1) A. *monticolus*, (2) A. *lundbladi*, (3) A. *chilensis*, (4) A. *caledonia*, (5) A. *circularis*, (6) A. *tabberabbera*, (7) A. *tolarda*, (8) A. *tasmanica*, (9) A. *arraphus*, (10) A. *partitus*, (11) A. *zelandicus* [Fig. 1 from Cook (1988), other Figs. from original descriptions as given under "Species included"].
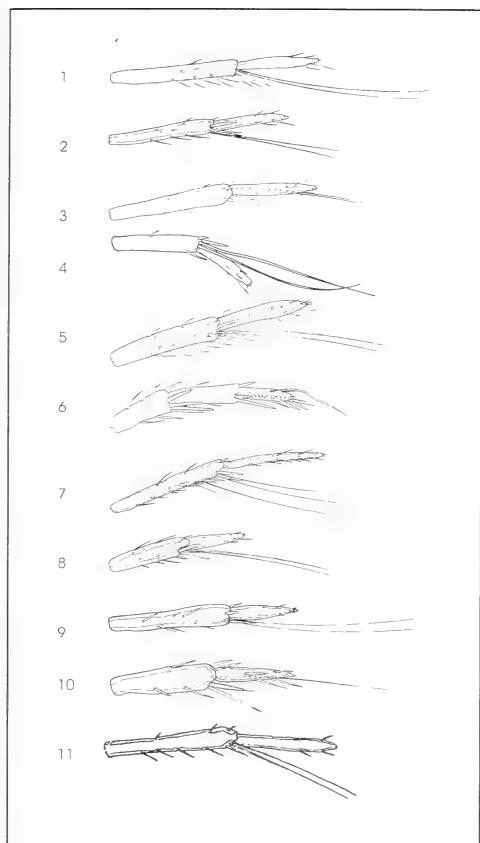
FIG. 71. Shape of IV-L-5,6 in *Anisitsiellides*: (1) *A. monticolus*, (2) *A. lundbladi*, (3) *A. chilensis*, (4) *A. caledonia*, (5) *A. circularis*, (6) *A. tabberabbera*, (7) *A. tolarda*, (8) *A. tasmanicus*, (9) *A. arraphus*, (10) *A. partitus*, (11) *A. zealandicus* [Fig. 1 from Cook (1988), other Figs. from original descriptions as given under "Species included"].

the Anisitsiellinae in a separate genera group for the following reasons: (1) Chelicera with a prominent, rounded elevation at the proximal end of the basal segment (not depicted so in *A. tabberabbera*). The only other genus for which a chelicera with a similar shape is described is *Sigthoriella*. It is similar to the strong and pointed, dorsal elevation in the middle basal segment found in the Bandakiinae. (2) Sutures C3/C3 and C4/C4 medially present and GF with anterior border posterior to insertions of IV-L. (3) IV-L-5 with 1–3 clearly elongated thin setae (swimming hairs) distally.

Genus: *Zelandatonia* Cook, 1992 [1 sp.]

Typus generis: *Zelandatonia orion* Cook, 1992. Location of genotype: CNM. No material examined.

Definition (adults)

Characters of the Anisitsiellinae as defined above and:
* All four coxal groups close together but not fused; anterior coxal groups extremely small compared to posterior coxal groups.
* C4 extended well posterior off the genital field and almost united medially.
* GF with anterior border at level of insertions of IV-L.
* Insertions of IV-L with condyles.
* IV-L with claws reduced to small spines.
* IV-L-5 distally with 5 clearly enlarged thin setae (swimming hairs).

Species included

Zelandatonia orion Cook, 1992 was discovered as a single female only in samples from driven wells in New Zealand.

Inventory (adults)

DS/VS. DS/VS absent. Dorsum with two pairs of very small platelets, the anterior pair of which bear the postocularia. Venter with excretory pore situated on a small rounded sclerite.
Eyes. Not described in Cook (1992).
Coxae. See definition. A pair of setae on small bases closely adpressed to posterior end of C4. Suture C3/C4 incomplete, extending approximately half-way to midline.
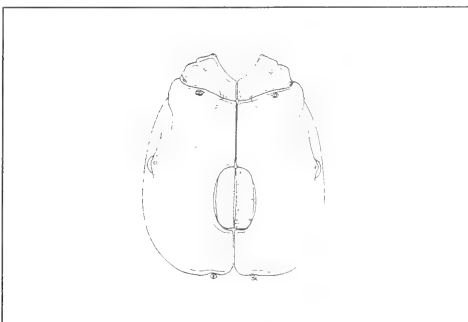
FIG. 72. *Zelandatonia orion* Cook, 1992: Shape of coxal groups, with C4/C4 adpressed to each other posterior to the genital field [Fig. from Cook (1992)].

Cg4. Cg4 on C3, near mid-length of suture C2/C3.

GF. See definition.

Ac. Three pairs Ac in two rows; no gaps between first, second and third pair.

I-L-6. I-L-6 with setae reduced to hairs; claws with blade and clawlet.

IV-L-5,6. IV-L-6 with claws reduced to small spines. Lateral rows of 2-4 small setae are present in most species. Five swimming hairs (about as long as IV-L-6) insert at the distal end of IV-L-5.

Palpus. Dorsal length of P1-5 [in μm]: 24, 104, 59, 102, 31; P2 and P3 noticeably swollen and oval in outline. P4 without ventral tubercles, claws at P5 small.

Chelicerae. Total length of chelicerae 170 μm (no further information in Cook 1992).

Taxonomic placement

I suggest placing *Zelandatonia* in the *Anisitsiellides*-group for the following reasons: *Zelandatonia* shares with *Anisitsiellides* the elongated swimming hairs at IV-L-5, the genital field placed quite far posteriorly, the claws with blade and clawlet on the first three pairs of legs, the condyles at the insertions of the IV-L. The character "anterior coxal groups very small compared to posterior", is also found in *Anisitsiellides tolarda*. Among the species included in *Anisitsiellides*, *A. tolarda* is closest to *Zelandatonia orion*, being less sclerotized than the other members of the genus (with eye-plates not fused medially). *Anisitsiellides tolarda* and *A. tabberabbera* share the position of the Cg4 posterior to suture C2/C3 with *Zelandationa*. A palp with swollen P2 and P3 is present in *Anisitsiellides caledonia* (however in this species P4 is equipped with large ventral tubercles). Hence the only major differences between *Anisitsiellides* and *Zelandatonia* are (1) the lesser secondary sclerotizations of the latter, and (2) the contribution of the fourth coxae to the stabilization of the area directly posterior to the genital field (an area otherwise stabilized by secondary sclerotizations arising from the postgenital plate, the excretory pore plate, and the borders of the fourth coxae). There is no information given if the chelicera of *Zelandatonia* possess the prominent posterior elevation on the basal segment found in *Anisitsiellides*.

Genus: *Sigthoriella* Besch, 1964 [1 sp.]

Typus generis: *Sigthoriella hygropetrica* Besch ,1964. Location of genotype: SMF (?). No material examined.

Definition (adults)

Characters of the Anisitsiellinae as defined above and:
- Chelicerae with dorsal elevation at proximal end of the basal segment.
- Claw at I-L-6 with ventral blade and clawlet.
- IV-L-6 with well-developed hook-like claws; insertions of IV-L without condyles.
- GF with anterior border at the level of insertions of IV-L.
- C4 with posterior suture and secondary sclerotization present.
- Cg4 just posterior to suture C3/C2; sutures C3/C4 medially reduced.

Species included

Sigthoriella hygropetrica Besch, 1964 was discovered as a single specimen in the dump area next to a spring in Valdivia (Chile).
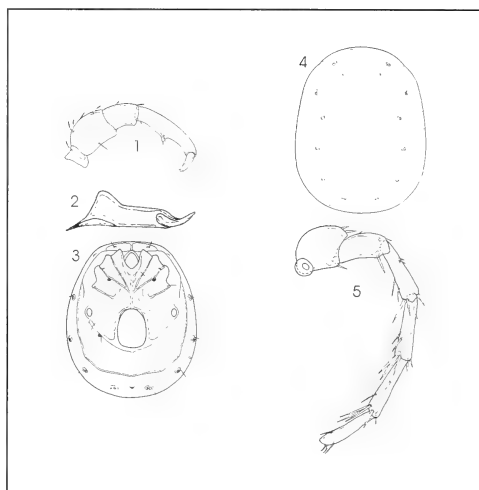
FIG. 73. *Sigthoriella hygropetrica* Besch, 1964: (1) palpus, (2) chelicera, (3) ventre, (4) dorsum, (5) IV-L [Figs. 1, 3-5 from Cook (1988), Fig. 2 from Besch (1964)].

Inventory (adults)

DS/VS. DS/VS absent. Dorsum without platelets. Venter with posterior secondary sclerotization extending about half-way from posterior border of C4 and the GF to posterior end of body. The anterior portion of the ventral shield is formed by a pair of platelets.

Eyes. Lenses of lateral eyes not in capsules and not attached to the pair of platelets situated anterior to the ventral shield, but found in the cuticle at extreme anterolateral edges of the dorsal shield (fide Cook, 1988).

Coxae. See definition.

Cg4. Cg4 on C3, near mid-length of suture C2/C3.

GF. See definition.

Ac. Lost during slide-making. Cook (1974) found one acetabulum in the holotype slide and assumes that 3 or 4 pairs are present.

I-L-6. I-L-6 possessing claws with blade and clawlet.

IV-L-6. See definition.

Palpus. Dorsal length of P1-5 [in µm]: 18, 76, 52, 107, 10; P2 with a heavy ventral seta inserted somewhat along the side of the segment; P4 with two well-developed ventral tubercles beside each other; claws at P5 small.

Chelicerae. Total length of chelicerae 148 µm; length of cheliceral claw 44 µm.

Taxonomic placement

Sigthoriella, discovered with a single female specimen in Valdivia in Chile, bridges the gap between the Bandakiinae and the *Anisitsiellides*-group of the Anisitsiellinae in its combination of characters: A chelicera with a rounded, prominent dorsal elevation on the proximal end of the basal segment is typical of *Anisitsiellides* but not found in the Bandakiinae. The organization of the coxae is similar to several species of *Anisitsiellides* (e.g., *A. monticolus*, *A. tabberabbera*), and differs from the Bandakiinae in that there is no paramedian suture separating off a platelet medial to C3. Well-developed claws at IV-L are found in all members of the Bandakiinae but not in *Anisitsiellides*. A well-developed dorsal shield is found in Bandakiinae and *Anisitsiellides* but not in *Sigthoriella* (and the dorsal shield is reduced to four small platelets in *Zelandatonia*). One or two platelets which seem to cut off an anterior portion of the ventral shield (and in most are carrying eye lenses) are found in both *Anisitsiellides* and Bandakiinae. In *Sigthoriella* they are present, but the eye-lenses are situated laterally from these platelets in the cuticula.

The genus *Sigthoriella* is here tentatively assigned to the *Anisitsiellides*-group for the shape of its chelicaera being similar to that generally found in *Anisitsiellides* but is not found in any other Anisitsiellinae.

Nilotonia-group

Cook (1974) points out that the "soft bodied" Nilotoniinae grade into the "highly sclerotized" Anisitsiellinae (sensu Cook 1974), and places *Mamersella* and *Anisitsidartia* under the Anisitsiellinae. He points out that the presence of a broad dorsal furrow connects them with the less sclerotized Nilotoniinae (*sensu* Cook 1974) and separates them from the other members of the Anisitsiellinae (*sensu* Cook 1974) which possess tightly fitting dorsal and ventral shields and a narrow dorsal furrow.

This continuum of species, with a gradual change in the extent of their sclerotizations, is even more complete since Bader (1995) described several highly sclerotized species from Trinidad, which are included in *Nilotonia* (*Mamersonia*) in this study.

As a consequence of the descriptions of new species, today the placement of several species in *Nilotonia*, *Mamersella* and *Rutacarus* is arbitrary. Since only additional information on larval stages will elucidate their phylogenetic relationships, I have left most of the species with "doubtful" placement as "species incertae sedis" under the genera where they were placed in the original descriptions.

The description of larvae of the "highly sclerotized" *Anisitsiella costenus* by Cramer & Smith (1993), and of the "soft bodied" *Nilotonia longipora* and *Nilotonia tegulata* by Gerecke & Smith (1993), made clear that these three species are closely related to each other. Comparison with the larvae of *Limnesia* shows several common characters as well (see discussion under Limnesiidae). Thus, larval characters suggest treating Nilotoniinae as junior synonym to the Anitsiellinae and placing several genera of the resulting subfamily next to the Limnesiinae.

The genera placed in the *Nilotonia*-group share characters such as (1) a *Dartia*-like or *Nilotonia*-like chelicera without a prominent elevation on the basal segment, (2) claws on first three pairs of legs simple and hook-like, sometimes with ventral or dorsal clawlet and in several species with a series of ventral clawlets, but never with a ventral blade and bladelet such as for example in *Anisitsiellides*, (3) palpus typically "anisitsiellid-like", but a micropalpus is found in *Anisitsidartia* and an untypical palp is found in *Rutacarus pyriformis*.

Several characters indicating a close relationship to other subfamilies of the Limnesiidae are found in Anisitsiellinae only in the *Nilotonia*-group, such as (1)

enlargement of the basal sclerite carrying the acetabula, including the fusion of these sclerites, in several species of *Nilotonia* (*Dartia*), (2) reduction in the size of the acetabula, with a large gap between first and second pair (such a gap, along with comparatively smaller acetabula, is commonly found in *Limnesia* (s.s.)), and (3) seta on ventral side of P2 on a short tubercle.

Genus: *Anisitsidartia* Cook, 1966 [1 sp.]

Typus generis: *A. micropalpis* Cook, 1966. Material examined: *A. micropalpis*, male, slide 4690, SMF. Location of types: Holotype: CNM (?).

Definition (adults)

Characters of the Anisitsiellinae as defined above and:
- Dorsal shields completely covering dorsum, but separated into an anterior and a posterior shield with two pairs of glandularia lateral to the posterior shield in the dorsal furrow.
- Palpus very small with total length about one sixth of the total length of the dorsal shields (total length of palpus is 120–140 μm compared with 700–900 μm total length of the DS and 130–160 μm of the chelicerae).
- VS complete, but with a narrow gap between the secondary sclerotization of the postgenitale and the secondary sclerotization posterior to C4.
- IV-L-6 with claws reduced, with 10–15 short lateral setae and one long terminal seta (Fig. 75).
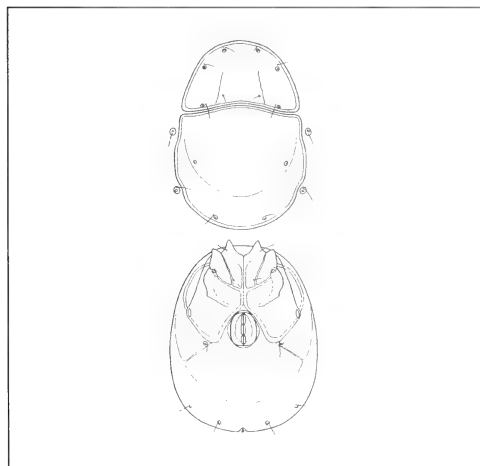
FIG. 74. *Anisitsidartia micropalpis* Cook, 1966: Dorsal shield (top), ventral shield (bottom) [Figs. from Cook (1966)].

Species included

Anisitsidartia micropalpis Cook, 1966, reported with a female from a stream in West Africa (Bomi Hills road, 6 miles north of Bushroad Island, Zaire/Congo), is the only known species of the genus. Viets & Böttger (1974) report the male from another stream in the region (Nyamitalo near lake Kivu).

Inventory (adults)

DS/VS. See definition.

Eyes. Eyes most probably fused into the ventral shield (no information in the publications of Cook and Viets). The position of the eyes could not be seen clearly in the allotype in the Viets collection.

Coxae. First coxae fused medially, suture only weakly expressed. Suture C3/C4 incomplete.

Cg4. Cg4 situated posterior to the suture C2/C3, about one-third of the distance from the lateral border of C3.

GF. On both lateral sides of GF the secondary sclerotization leaves small areas open. A similar situation is found in *Paddelia* and *Anisitsiella.* Anterior border of GF at level of insertions of IV-L. Posterior border of C4 at level of posterior border of GF. C4 almost touching GF at anteromedial angle. Medial border of C4 not impending GF in middle and posterior parts.

Ac. Three pairs of Ac of equal size, no gap between first, second and third Ac.

I-L-6. Claws thin and hook-like (Fig. 75); I-L-6 without setae and equipped with a few hairs only.

IV-L-6. See definition. Cook depicted a IV-L-5,6 with the long terminal seta broken (Cook 1974, p. 561, Fig. 414). A leg with the complete seta is shown in Fig. 75.

Palpus. Palpus with "swollen" segments. Most setae of P2 and P3 are longer than the dorsal length of the respective segments. The below given data for the dorsal length (d.l.) of the segments and other features of the palpus are taken from Cook (1966) and Viets (1974). P1 without seta and with a d.l. of 20–24 μm. P2 with ventral seta absent (!), with 2 dorsal setae, and with a d.l. of 38–42 μm. P3 with 3 dorsal setae and with a d.l. of 21–24 μm. P4 with 1 small, dorsodistal setae, 2 ventrodistal hairs, and with a d.l. of 35–39 μm. P5 with "long" claws (4 μm of length of P5) and with a total d.l. of 10–14 μm. Total length of the palpus is 128–139 μm.

Chelicerae. Total length of chelicerae 128 μm in the male and 159 μm in the female.
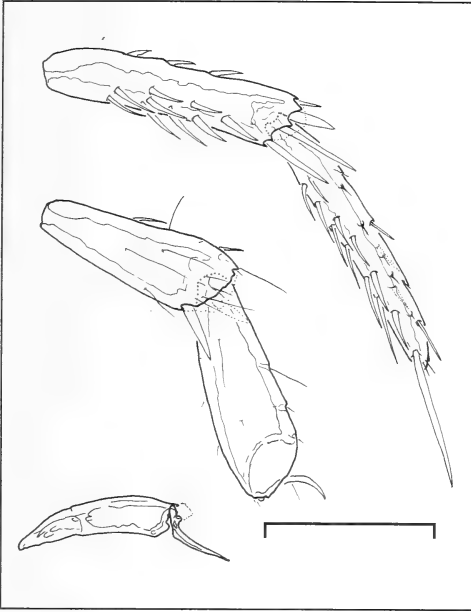
FIG. 75. *Anisitsidartia micropalpis* Cook, 1966 allotype (male): IV-L-5,6 (top), I-L-5,6 (middle), chelicerae (bottom) [Scale bar = 100 μm].

Taxonomic placement

A DS organization similar to that of *Anisitsidartia* (DS appearing to be divided into an anterior and a posterior half, together covering most of the surface of the dorsum) is known in a few genera of the Limnesiidae (e.g., *Psammotorrenticola, Stygomamersopsis*, some species of the *Nilotonia*-group, *Tubophorella, Neomamersa, Meramecia, Nicalimnesia*, and in males of *Shivatonia* gen. nov. and *Bharatonia*).

A nearly complete VS, with narrow gaps between the secondary sclerotization posterior to the genital field, and the secondary sclerotization posterior to C4, is found in several species of the *Nilotonia scutata*-like species (e.g., *N. scutata, N. testudinata, N. biscutata, N. amazonica*).

A strikingly small palpus, as found in *Anisitsidartia*, has been noted for several species among the early derived Hygrobatoidea (s.T.). Small palps are found in different taxa (e.g., *Psammolimnesia mexicana, Neoatractides inachus, Africoxus szalayi, Torrenticola suvarna, Pseudotorrenticola mitchelli*).

Some species of the family Torrenticolidae possess rather small palps. In some other species with small palps (e.g., *Tubophora, Psammotorrenticola*) a camerostome is developed, allowing the tracing of prey in the interstitial environment. In *Anisitsidartia* no camerostome is present.

While in other taxa, e.g., genera of the Torrenticolidae, single species among several others of the genus does possess a small palpus, in *Anisitsidartia* a separate genus has been erected for the species with the unusual palp.

The small palpus is the only character fully distinguishing *Anisitsidartia* from certain species of the genus *Nilotonia*, especially from the *Nilotonia scutata*-like species.

To describe, what is a "small" palpus the ratio of total length of palps to total length of genital flaps is taken. In *Nilotonia indica* (Anisitsiellinae Limnesiidae) this ratio is 2.0, while in *Anisitsidartia micropalpis* it is 0.9. Two other forms with a "small" palpus are (1) in the monotypic genus *Psammotorrenticola gracilis* (Anisitsiellinae Limnesiidae) were this ratio is 1.5, and (2) *Tubophorella australis* (Limnesiinae Limnesiidae) where it is 1.1.

Until nymph and larvae of the species are known, the position of the genus *Anisitsiella* will remain doubtful. It is here kept tentatively under the Anisitsiellinae.

Genus: *Anisitsiella* Daday, 1905 [2 spp.]

Typus generis: *Anisitsiella aculeata* Daday, 1905. Material examined: *Anisitsiella aculeata* [holotype] NMB. *Anisitsiella* [= *Mamersellides*] *ventriperforatus*, coll. K.O. Viets, SMF, (approx. 20 specimens from different locations). Location of t.g.: NMB.

Definition (adults)

Characters of the Anisitsiellinae as defined above and:
- Three pairs of Ac below movable genital flaps and a pair of holes in the ventral shield. These holes located lateral to the anterior outer border of the genital flaps. They were called "Genitalporus" by Daday (1905) and were mistaken as for a fourth pair of Ac in many publications.
- Eye lenses of lateral eyes with (1) anterior pair near the anterior lateral edges of the ventral shield in males and free in the dorsal furrow in females, and with (2) posterior pair of eyes situated near anterolateral corners of the dorsal shield with their lenses elongated and surrounded by a perforated ring-like platelet.
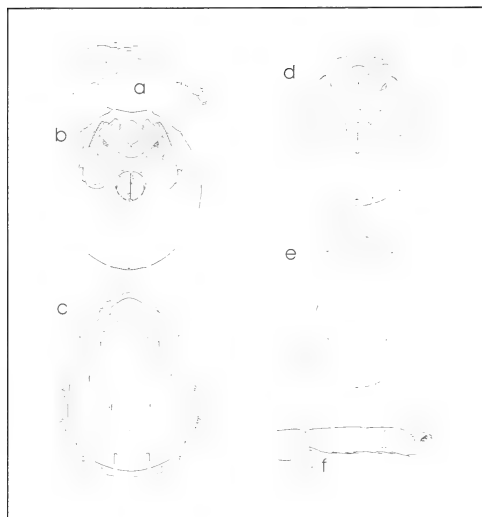
FIG. 76. *Anisitsiella costenus* Cramer & Smith, 1993: (a) palpus, (b) DS (female), (c) VS (male), (d) DS (male), (e) VS (female), (f) 1-L-6 (male) [Figs. from Cramer & Smith (1993)].

- Thin, stiff, elongated "swimming setae" present on IV-L (in some taxa also on distal segments of other legs).
- DS complete, undivided, with 6 to 8 pairs of glandularia.

Taxa included

I propose to treat *Mamersellides ventriperforatus* Lbld., 1937 as a junior synonym to *Anisitsiella aculeata* Daday, 1905. The typus generis to *Anisitsiella* Daday, 1905, was rediscovered in the NHB during the investigations for this study. It further turned out that the figures and the German text of the original description were misinterpreted in most of the later published works (see below).

Species included

(1) *Anisitsiella aculeata* Daday, 1905 [new syn. = *Mamersellides ventriperforatus* Lbld., 1937] is a common and widespread species in standing (or slow-flowing) water bodies in South America (Paraguay, Brazil, Argentina, Uruguay).
(2) *Anisitsiella costenus* Cramer & Smith, 1993 is reported from the same type of habitats in Central and North America (Mexico, Florida).

Inventory (adults)

DS/VS. DS/VS complete; anterior border of DS appears straight in males of the genus due to ocular platelets and/or eye-lenses being adpressed to it in anterolateral position.
Eyes. No information on the position of the eyes or their fusion to DS or VS is given in the text of the original description by Daday (1905). It is impossible to make out their position in the slide of the type specimen. Adequate figures were produced by Lundbald (1941) and by Cramer & Smith (1993).

The figures given by Daday (1905) show well the situation found in the males of *Mamersellides*. The two lenses of the lateral eyes are not placed together in a common capsule, but the medial lens is large, round and situated close to the ventral shield, whereas the lateral lens is elongated and perforates a small platelet. The pierced platelet is more or less adpressed to the corner of the dorsal shield and protruds in an anterolateral direction in males, forming anterolateral edges, whereas in the females the ocular platelets are smaller and not adpressed to the anterolateral corner of the dorsal shield, and the anterior border of the dorsal shield is rounded (Fig. 76, Fig. 78).
Coxae. The organization of the coxae is shown in Fig. 76. C1/C1 are fused medially while C3 and C4 are medially free without common suture. Possibly Da-
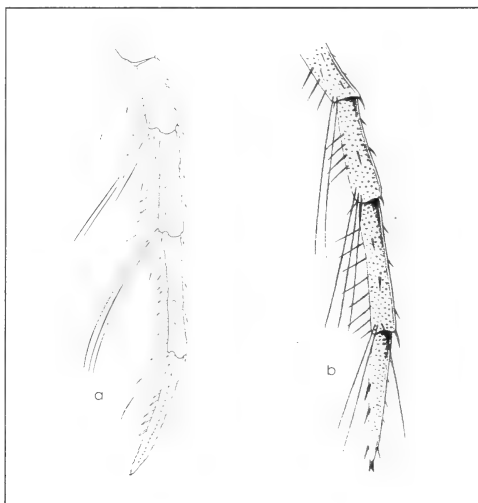
FIG. 77. *Anisitsiella*: IV-L-2-6. Fig. a: *A. costenus*, Fig. b: *A. aculeata* [Fig. a from Cramer & Smith (1993); Fig. b from Daday (1905)].

day (1905) has drawn the inside view of the venter, so that in his figure (Daday 1905, p. 297) all coxae (C1-C4) appear to be medially free.

GF. Anterior border of GF on level of insertions of IV-L. Daday (1905) reports for the type specimen three pairs of Ac and a pair of holes in the ventral shield located at the anterior outer border of the genital flaps called "Genitalporus" by Daday. The impression of holes is given by the VS retreating in this area from the genital flaps. A similar situation is found for example in *Paddelia* and *Anisitsidartia.*

I-L-6. Claws hook-like. In one species claws with a series of minute ventral clawlets and a dorsal clawlet on the first leg (the clawlets increase in size from I-L to III-L).

IV-L-6. Claws reduced to small setae. Series of insertions of minute hairs at IV-L-6 may be present.

SW-H: Enlarged swimming setae present at the distal end of IV-L-3,4,5.

Palpus. "Anisitsiellid-like" palpus. P1 with dorsal seta present, P2 with ventral seta shorter or about as long as ventral length of the segment, P4 ventrally with small tubercles and 4 setae, P5 small with 3 minute claws and 2 setae.

Chelicerae. Dartia-like chelicera, without a strong elevation on the dorsal border of the basal segment.

Taxonomic placement, synonyms, discussion of species

A male of *Anisitsiella aculeata* reported by Daday (1905) from Paraguay (S. America) was treated as the only known specimen of the genus until now. A similar species, *Mamersellides ventriperforatus* Lundblad, 1937, first described from a single female, was frequently found with males and females in ponds in southern Brazil and in standing water habitats in Columbia, Paraguay and Argentina (Lundblad 1941, Lunblad 1953, Viets 1954, Ferradas 1980). Cramer & Smith (1993) described and discussed the larvae and adults of a further species, *M. costenus.* This species was discovered in ponds, marshes and backwater pools of streams in Colima and Veracruz states (Mexiko) and Florida (USA). Cook (1974) as well as Cramer & Smith (1993) assumed *Mamersellides* to be a junior synonym of *Anisitsiella.* However, they supposed that the holotype of *Anisitsiella* was lost and regarded the original description as inadequate and incomplete. They suggested not synonymizing the two genera until topotypical specimens were collected and studied.
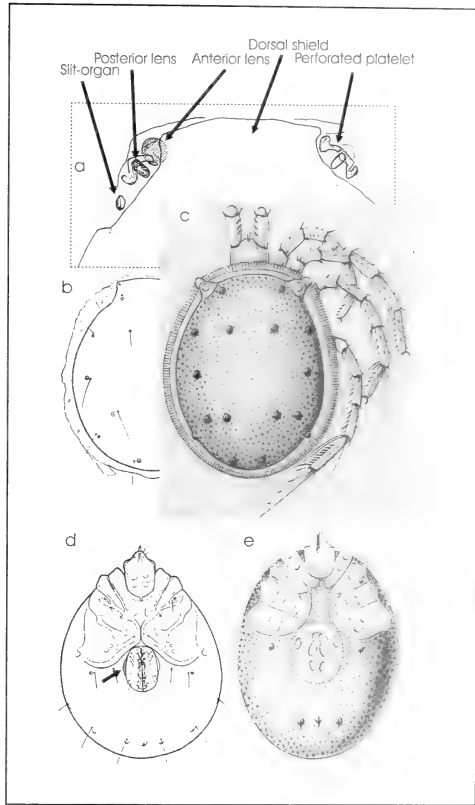
FIG. 78. *Anisitsiella aculeata* (male): (a) eye region, (b) left half of DS, (c) dorsal view, (d) and (e) ventral view. The arrow in (d) indicates the position of the opening lateral to the genital flap (marked gray on the left side of the figure) [Fig. a, original drawing from Präp. 7480, coll. K. Viets, SMF; Figs. b and d from Lundblad (1937); Figs. c and e from Daday 1905].

The holotype specimen of *A. aculeata* was recently rediscovered in the collections of the NMB. It is, however, in a very poor condition, being mounted on a slide on which 50% of the mounting medium is dried up and the black sealing solution has entered under the cover slide. Framed by the dark sealing solution, the area of the holotype specimen is now the only area were remains of the light yellow mounting fluid can be found. Unfortunately the type specimen itself has faded so much that only under severe difficulties can chitinous parts be distinguished from artifacts.

Misunderstanding Dadays (1905) German description, Cook (1974) and others believed that *Ani-*
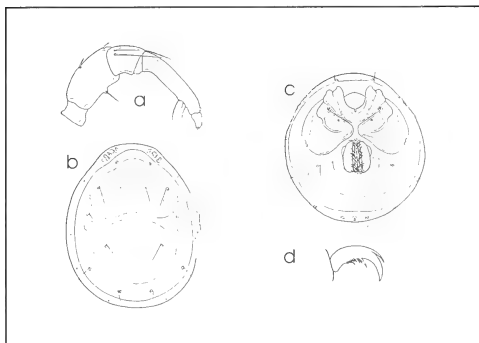
FIG. 79. *Anisitsiella aculeata* (female) [Figs. from Lundblad (1941)].

sitsiella aculeata has 4 instead of three pairs of acetabula. However, Daday gives detailed figures and a detailed generic description: "..., genital opening with half-moon-like genital flaps on each side. On their inner side 3 acetabula in a row, outside of them, on each side, one large 'genital pore'." "..., die Genitalöffnung an beiden Seiten durch halbmondförmige Genitalklappen begrenzt, am Innenrande derselben stehen je drei Genitalnäpfe übereinander, neben ihnen an beiden Seiten aber liegt je ein großer Genitalporus." (Daday, 1905, p. 297). Viets (1954) reports *Mamersellides ventriperforatus* as a wide-spread species in the Amazon region. Dadays (1905) description of *Anisitsiella* hardly differs from the description of *Mamersellides* by Lundblad (1941).

After confirming the fact that *Anisitsiella* possesses 3 instead of 4 acetabula, the remaining differences certainly do not justify an independent generic status for *Mamersellides*. I therefore suggest that *Mamersellides* Lbld., 1937 is a junior synonym of *Anisitsiella*. The chances are slight that Daday (1905) has described a rare species never found again since then. Hence I suggest ignoring the small differences between the descriptions of Daday (1905) and Lundblad (1937, 1941) and treating *Mamersellides ventriperforatus* Lbld., 1937, as a junior synonym of *Anisitsiella aculeata* Daday, 1905.

Differences between the females of the two species are found (1) ventrally in the shape of the slightly elevated area posterior to the genital field, and in that the coxae flank the genital field more closely in *A. costenus*, and (2) dorsally in that the slightly elevated area of the DS is further from the posterior end of the DS in *A. costenus* than in *A. aculeata* (cf. Cramer & Smith 1993).

As discussed under Limnesiidae: larval characters show the close relationship between *Nilotonia*, *Manotonia* and *Anisitsiella*. In adults, the relation with the Nilotonia-group is expressed through the shape of the chelicera and through the claws of the first three legs being typically equipped with a comb of ventral clawlets.

Cramer & Smith (1993) suggested treating, the slightly elevated areas of the dorsal shields as homologous to the separate plates located in these areas in the adults of *Nilotonia* and other genera of the "anisitsiellid-like" mites.

Genus: *Mamersella* Viets, 1929 [2 subgenera, 4 spp.]

Typus generis: *M. thienemanni* Viets, 1929. Material examined: *M. thienemanni* 4 females and 3 males from the Himalayas, collections "Ind 30/93" and "Ind 33/93," CAP; *M. thienemanni* female [paratype] Präp. 4503 SMF; (*Platymamersopsis N. tototaensis* male [allotype] Präp. 4713 in SMF); (*M. anomala* female [paratypes] Präp. 3657, 3658; SMF = *L. auspexa* Cook, 1983; NOT *L. anomala* Koenike, 1895). Location of t.g.: SMF

Definition (adults)

Characters of the Anisitsiellinae as defined above and:
- VS and DS complete; DS undivided, including no, few, or many glandularia.
- Palpus anisitsiellid-like. P1 without dorsal seta.
- I-L-6 with hook-like claws; with or without several small ventral clawlets; with or without dorsal clawlet.
- IV-L-6 with claws absent or reduced to small setae.

Subgenera and species included, distribution and habitats

Subgenus: *Mamersella*

1. *M.* (*M.*) *thienemanni* Viets, 1929, reported from a spring near Tobago and from mosses in the River Kali (Sumatra), is the type species of the genus. Lundblad (1971) reports this species from Java. During field work for the present study further specimens were discovered in a well near Rishikesh (upper catchment area of River Ganga, northern India).

2. *M.* (*M.*) *maryellenae* Cook, 1967 – a second oriental species – was described from a cataract on the road between Ootacamund and Kotagiri (Madras state, India) and in a small river near the Kerala-Mysore border in India.

Moving subgenus *Neomamersella* to genus *Platymamersopsis*

Cook (1966) described *M. tototaensis* from a small stream in West Africa (Zaire, Congo) and described the subgenus "*Neomamersella*" for this species. I propose to shift this species and subgenus to *Platymamersopsis*. The reasons are discussed below and in the chapter "*Platymamersopsis.*"

Moving *Mamersella anomala* to *Limnesia*

The species described as *M. anomala* by Hopkins (1967) was collected from a river in New Zealand. Investigation of type material reveals that it belongs to *Limnesia* (see discussion below.).
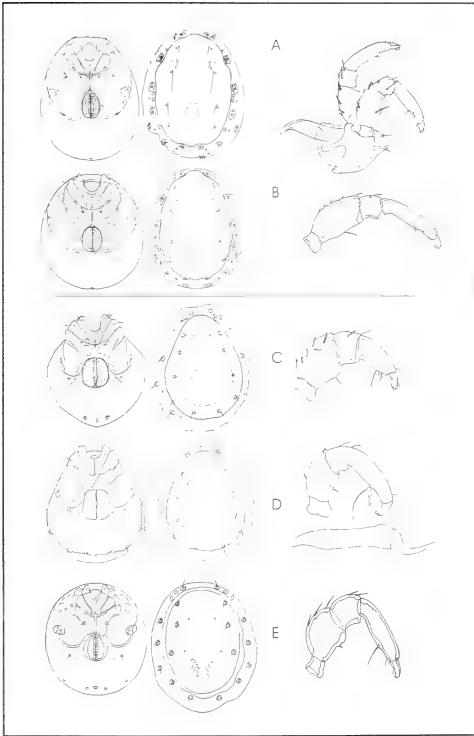
FIG. 80. Genus *Mamersella* VS, DS, palpus, chelicera. *Mamersella* (*s.s.*): (A) *M.* (*M.*) *thienemanni*, (B): *M.* (*M.*) *maryellenae*; *incertae sedis*: (C) (i.s.) *M. mesoamericana*, (D) (i.s.) *M. ponderi*; *Limnesia*: (E): *L. auspexa* [Figs. modified. Fig. A from Viets (1935), Fig. B from Cook (1967), Fig. C from Otero (1987), Fig. D from Harvey (1990), Fig. E from Hopkins (1967)].
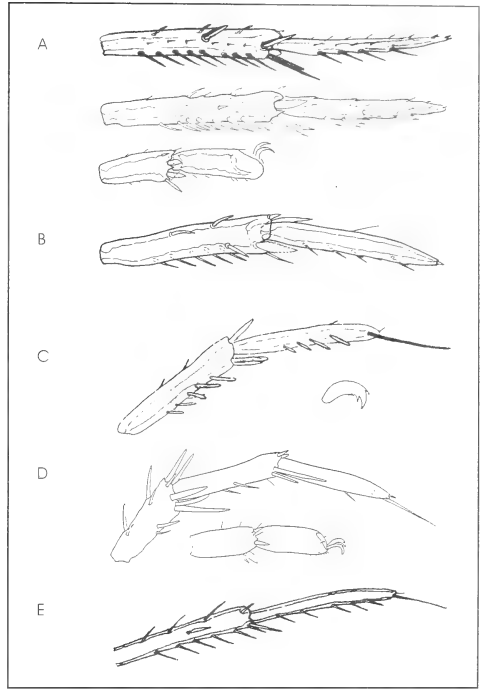
FIG. 81. Genus *Mamersella* IV-L-5,6 and I-L-5,6. (A): *M.* (*M.*) *thienemanni* IV-L [Fig. from Viets 1935] (top), IV-L-5,6 original (middle), I-L-5,6 original (bottom). (B): *M.* (*M.*) *maryellenae* IV-L-5,6 (from Cook 1967); (C): (i.s.) *M. mesoamericana* IV-L-5,6 and claw of III-L (from Otero 1987); (D): (i.s.) *M. ponderi* IV-L-5,6 and I-L-5,6 (from Harvey 1990); (E): Genus *Limnesia*, *L. auspexa* IV-L-5,6 (from Hopkins 1967).

Species incertae sedis

Two species cannot be distinguished from species placed under *Nilotonia* (*Mamersonia*). These are *M. mesoamericana* Otero, 1987, described from Central America, and *M. ponderi* Harvey, 1990, described from Finniss Spring in South Australia (see discussion below).

Inventory:

DS/VS. VS and DS complete.
Eyes. Eyes lying free in the dorsal furrow in *Mamersella* (s.s.). The nasal plate of *M.* (*M.*) *thienemanni* is described below. A slit organ and small sclerites accompany the posterior pair of lenses in some species.

Coxae. Suture C3/C4 incomplete. Posteromedial edge of C4 round.

Cg4. Cg4 is (1) absent in *M. ponderi*, (2) clearly posterior to suture C2/C3 but still close to it in *M. (M.) thienemanni* and *M.* (s.s.) *maryellenae*, and (3) close to anterior border of GF in *M. mesoamericana*.

GF. C4 closely flanks the GF and the posterior border of C4 reaches the level of the posterior border of the GF in *Mamersella* (s.s.) In the species "incertae sedis", C4 does not impend the GF closely, reaching about the middle of it.

Ac. Three pairs of Ac of equal size in *Mamersella* (s.s.) and in some of the species "incertae sedis." Gap between first and second Ac longer than length of Ac in *M.* (i.s.) *ponderi* Harvey, 1990.

I-L-6. Simple claws, hook-like and (1) without ventral or dorsal clawlets in *Mamersella* (s.s.), (2) with

FIG. 82. *Mamersella thienemanni*: Anterior portion of dorsal shield with nasal plate and eye region (top), dorsum (bottom). Note: the two figures are turned by 180° against one another [DS = dorsal shield].

dorsal clawlet in *M.* (i.s.) *ponderi*, and (3) with ventral clawlets and dorsal clawlet in *M.* (i.s.) *mesoamericana*.

IV-L-6. Without swimming hairs. With claws reduced or small and (1) without long terminal seta in *Mamersella* (s.s.), or (2) with long terminal seta in the other species.

Palpus. Palpus (1) "anisitsiellid-like" and slender in *Mamersella* (s.s.) and *M.* (i.s.) *ponderi*, or (2) "anisitsiellid-like" and robust in *M.* (i.s.) *mesoamericana*.

Discussion of species

In this study, the two species *M. thienemanni* and *M. maryellenae* are placed in the subgenus *Mamersella* (s.s.). They are similar to each other regarding shape and chaetotaxy of palps and legs, shape of coxae and chelicera (see figures above).

M. mesoamericana and *M. ponderi* are placed in this study as species "incertae sedis." They show more similarities to certain members of *Nilotonia* (*Mamersonia*) than to *Mamersella* (s.s.). Among the differences are: (1) the coxae C4 do not closely impend the genital field and do not extend to the posterior border of the genital field (as they do in *Mamersella* (s.s.)), (2) Cg4 is situated next to the suture C3/C2 in the species "incertae sedis" but well posterior to it in *Mamersella* (s.s.), and (3) IV-L-6 is equipped with a long terminal seta in the species "incertae sedis", while this seta is absent in Mamersella (s.s.).

M. mesoamericana differs from the other species in *Mamersella* in that its palpus is comparatively robust, and the ventral and dorsal shield do not extend to the lateral border of the body proper, leaving a wide furrow with soft integument.

M. ponderi differs from all other species in that the insertions of the IV-L possess condyles, and in the large gap between the first and the second pair of very small acetabula. Such a characteristic is found in all members of the genera *Dartia* and *Dartiella*. In fact, this species differs from *Dartiella* only in its extensive sclerotization.

Cook (1966) erected a new subgenus *Neomamersella* for the species *M.* (*N.*) *tototaensis*. The species differs considerably from *Mamersella* (s.s.). The similarities between them are restricted to the slender shape and small size of the dorsal shield (leading to a broad dorsal furrow with many glandularia pairs), and the absence of a long seta on IV-L-6. *M.* (*N.*) *tototaensis* shows several characters untypical of the *Nilotonia*-group and some of them suggest that the species should be treated as a "less sclerotized" form of *Platymamersopsis*. The characters include (1) an untypical
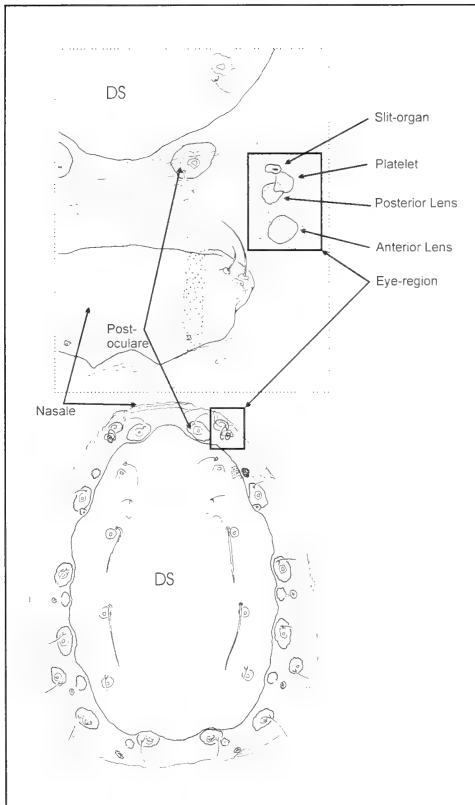
palp with P4 swollen and claws at P5 large and unfused, (2) a chelicera with a shape rather similar to that of *Platymamersopsis* and differing clearly from the shape otherwise typical of the *Nilotonia*-group, (3) a relative size, shape and chaetotaxy of IV-L-5,6 rather similar to that found in *Platymamersopsis*, with the IV-L-6 being only little longer than the I-L-6 in *M. (N.) tototaensis* (while in most *Nilotonia*-like species IV-L-6 is clearly elongated compared with I-L-6), and (4) the C4, which are more or less rectangular and with a ridge leading anteriorly from the insertions of IV-L to the insertions of III-L (as in *Platymamersopsis*). The subgenus *Neomamersella* is therefore moved to the genus *Platymamersopsis* in this study.

Mamersella anomala is a synonym of *Limnesia auspexa*
Limnesia auspexa Cook, 1983
Mamersella anomala Hopkins, 1967. Trans. R. Soc. N. Z. Zoology 10(4): 34
[Not *Limnesia anomala* Koenike, 1895]
Limnesia auspexa Cook, 1983. Contr. Amer. Ent. Inst. 21 (2): 23

The specimens described as *Mamersella anomala* by Hopkins (1967) do not belong to the genus *Mamersella*, but to *Limnesia*. According to the information on the slides of two female paratypes of *M. anomala*, found in the collection of K.O.Viets (SMF, slides 3657 and 3658), they were collected in a "swampy tributary of Waikanae river (New Zealand)." My examination showed that their acetabula are not placed below the flaps, but on the flaps. Other characters were checked and confirmed that these specimens belong to the genus *Limnesia*. The palpi show a shape typical of many Limnesiidae, with a peg-like seta on the ventral side of P2 situated on a small tubercle. A comparison of the female allotype of *M. anomala* with the female holotype of *Limnesia auspexa* Cook, 1983, both held in the Museum of New Zealand Te Papa Tongarewa (Wellington, New Zealand), made by Ricardo Palma (MONZ), has shown that these two specimens are conspecific. Therefore *M. anomala* and *L. auspexa* become synonyms. However, considering that the new combination *Limnesia anomala* (Hopkins, 1967) is preoccupied by *Limnesia anomala* Koenike, 1895, the name *Limnesia auspexa* Cook, 1983 becomes the valid name for this species. Cook (1983, p.24) in his discussion of the description of *Limnesia auspexa* stated that 'Specimens collected by Dr. Ceri Hopkins in a "swampy streamlet in the Waikanae River system, Tararua Mountains", North Island, also belong to this species.', but he neither mentioned *Mamersella anomala* nor the fact that the latter locality

is given by Hopkins (1967) as the locality for some of the other (paratype) material he examined and identified as *M. anomala*.

Genus: *Rutacarus* Lundblad, 1937 [2 subgenera, 5 spp.]

Typus generis: *Rutacarus pyriformis* Lundblad, 1937. Material examined: *Rutacarus (Eorutacarus) sasonus*, male [paratype] from coll. K.O. Viets, Präp. 7809, SMF. Location of t.g.: SMH

Definition (adults)

Characters of the Anisitsiellinae as defined above and:
- VS and DS complete; DS undivided, including four or five pairs of glandularia; VS closely impending GF and with posterior medial edge pointed and forming an angle less than 90°.
- Eye-lenses (1) with posterior pair either fused to postocular glandularium or free, and (2) anterior pair either fused on anterolateral edge to the upper border of the ventral shield or free.
- Palpus either P2 with two ventral setae and P4 swollen (as in *R.* (s.s.) *pyriformis*) or "anisitsiellid-like."
- I-L-6 either with claws hook-like or claws with a small ventral and dorsal clawlet.
- IV-L-6 with claws absent or reduced to small setae.
- IV-L-6 with or without long terminal seta and with a row of 2–4 medium-sized lateral setae.
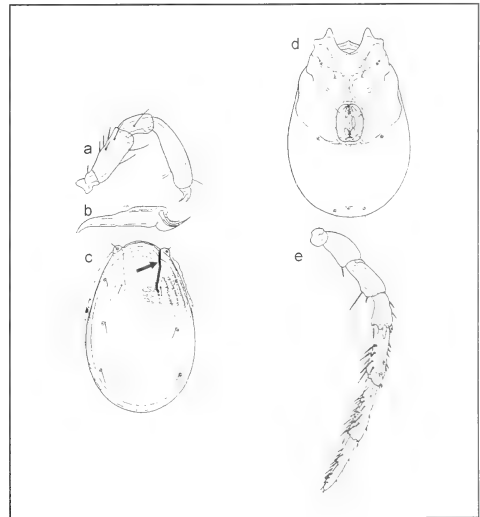
FIG. 83. *Rutacarus pyriformis* Lundblad, 1937: (a) palpus, (b) chelicera, (c) DS, (d) VS, (e) IV-L [from Lundblad (1941)].

Discussion of subgenera, species included, distribution and habitat

R. (s.s.) *pyrifomis* Lundblad, 1937, reported from a creek in southern Brazil, is the type species of the genus. While this species is strikingly different from all other genera of the Anisitsiellidae-Limnesiidae complex – due to the untypical palpus, the medially fused C1, and the ridge in the dorsal shield leading to the protruding eyes – the second subgenus, *R.* (*Eorutacarus*), erected by Cook in 1980, does not show such particular characters.

R. (*E.*) *ferradasae* Cook, 1980, from bottom deposits in small streams in Tucaman Province and Salta Province (Argentinia), is the species for which the subgenus *Eorutacarus* was erected.

R. (*E.*) *angelieri* Orghidan & Gruia, 1983 is described from a hyporheic sample collected from a mountain torrent in the "Parque Nacional Rancho Grande" (Estado Aragua, Cuba). Orghidan & Gruia

(1983) suggest the subgenus *Neorutacarus*, because of small differences in the extent of sclerotization of the ventral shield. However secondary sclerotizations vary greatly in extent, even between closely related species or male and female of a single species. Yet only the female of *R.* (*E.*) *angelieri* is known and the species is placed here in the subgenus *Eorutacarus*. However a particular characteristic of the species is the chitinized strip connecting the glandularia that are found in the dorsal furrow.

R. (*E.*) *sasonus* Cook, 1986 was discovered in a sample from a hole dug in a gravel bar in the Scamander River near upper Scamander, Tasmania (Australia).

Species incertae sedis

R. (i.s.) *stygius* Harvey, 1990 was discovered in Australia (near Victoria). While the other three members of *Rutacarus* (*Eorutacarus*) were collected from the hyporheic habitat, Harvey (1990) describes *R. stygius* as collected from the River Acheron. According to Harvey, *R. stygius* differs from the other members placed in *Rutacarus* in characters such as (1) C4 not impending genital field closely in posterior portion, (2) C4 with angle of posteromedial edge about 90° and edge rounded (angle less than 90° and edge +/– pointed in the other members of the genus), (3) dorsal shield without ridge, and (4) DS broader than in the other species.

On the position of lateral eyes and eye-lenses

Lundblad (1941) describes the lateral eyes as being incorporated into the ventral shield in *R. pyriformis*. According to Cook (1974) the eyes are incorporated into the glandularia platelets, which produces the characteristic bulging of the anterolateral portions of the dorsal shield. He erects the new subgenus *Eorutacarus* for *R.* (*E.*) *ferradasae*, in which both eye-lenses are incorporated into the ventral shield. Examination of paratype material in the collection of K.O. Viets reveals that in *R.* (*E.*) *sasonus* the medial eye is incorporated in the upper border of the ventral shield, while the lateral eye is lying free in the dorsal furrow. Harvey (1990), when assigning *R.* (i.s.) *stygius* to the genus, gives no information on the position of the eyes.
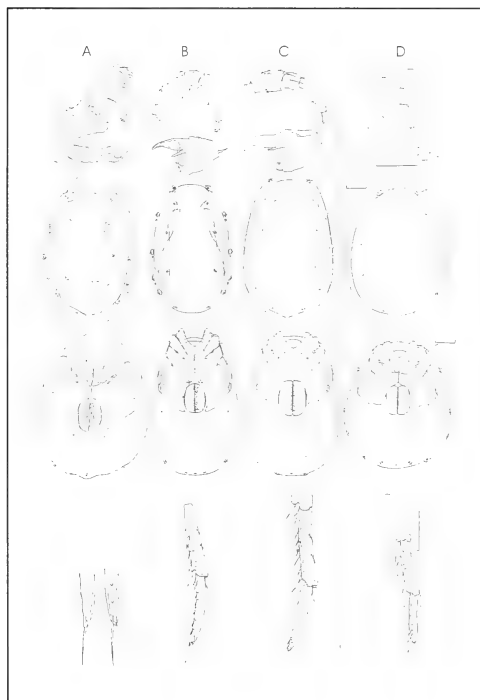
FIG. 84. Genus *Rutacarus*: (a) *R.* (*E.*) *angelieri*, (b) *R.* (*E.*) *ferradasae*, (c) *R.* (*E.*) *sasomus*, (d) *R.* (*i.s.*) *stygius* [Fig. a from Orgidhan & Gruia (1983), Fig. b from Cook (1980), Fig. c from Cook (1986), Fig. d from Harvey (1990)].

Inventory

DS/VS. VS and DS complete. With ridge in all species except *R.* (i.s.) *stygius*.

Eyes. see above.
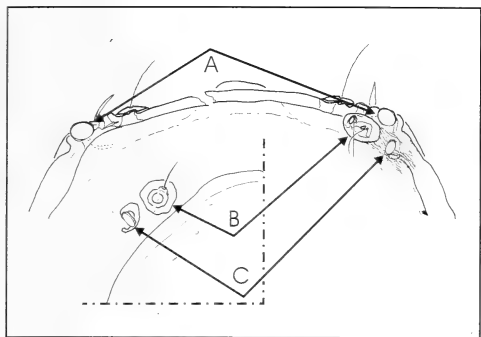
FIG. 85. *Rutacarus sasonus* dorsal view of anterior region: (A) anterior eye lenses, (B) glandular platelet, (C) posterior eye lenses.

Coxae. Suture C3/C4 incomplete (see also under GF).
Cg4. Cg4 is situated immediaetly posterior to the suture C2/C3 in all species.
GF. C4 closely flanks the GF in all but one species (*R. stygius*). The posterior border of C4 reaches the level of the posterior border of the GF in *R. pyriformis* and *R. ferradasae*, and about the middle of the GF in *R. stygius* and *R. sasonus.*
Ac. Three pairs of Ac usually of equal size and following close on one another. Gap between first and second Ac half the length of first Ac in the male of *R. ferradasae.* third pair smaller in *R. stygius.*
I-L-6. Simple claws, hook-like and (1) without ventral or dorsal clawlets in *R. pyrifomis,* or (2) with dorsal and ventral clawlet in subgenus *Eorutacarus.*
IV-L-6. Without swimming hairs. With claws reduced or small, a row of 2–4 medium-sized setae, and either (1) without long terminal seta in *R.* (s.s.) *pyriformis* and *R.* (i.s.) *stygius,* or (2) with a long terminal seta in the three other species.
Palpus. Palpus (1) "anisitsiellid-like" and slender in four species and (2) untypical of the Anisitsiellidae in *R. pyriformis* (with two ventral seta on P2). P1 in all species with a dorsal seta.

Further remarks

Nymphs and larvae unknown.

Genus: *Nilotonia* (Nordenskiöld, 1905)

Typus generis: *Nilotonia loricata* (Nordenskiöld, 1905). Synonyms: *Teutonia loricata*
Material examined: *Nilotonia amazonica,* female [holotype], slide 7292, SMF; *Nilotonia boettgeri,* female [holotype], "Ba-Sp 78/137", NHB; *Nilotonia boettgeri,* female, "Ba-Sp 78/135", NMB; *Nilotonia borneri,* female, [holotype], slide

xxi/54, NMB; *Nilotonia borneri,* male, "God dal Fuorn, NP 82/18," NMB; *Nilotonia buettikeri,* [type series], NMB, [= junior synonym to *N. robusta*]; *Nilotonia catarrhacta,* female, [holotype], slide 2966, SMF; *Nilotonia* cf. *robusta,* female, "Israel Aca 1124," slide 7091, SMF; *Nilotonia cooki* sp. nov., 1 female, "IND 90-69-PK:8"; 1 male, "IND Ec-3-90, 31. 12. 90"; *Nilotonia fundamentalis,* female, [holotype], slide "Golan, Meskus 24. 8. 1986, coll. ORTAL 66," NMB; *Nilotonia gracilipalpis,* male, [holotype], slide 3166, SMH; *Nilotonia gracilipalpis,* female [allotype], slide 3167, SMH; *Nilotonia indica,* male, [new allotype], "IND 25. 9. 90A" CAP [new record]; *Nilotonia longipora,* female, [type], "Algérie …, xii/99", NMB; *Nilotonia longipora,* female, [type], "Algérie …, xiii/02", NMB; *Nilotonia longipora,* female, "Gospic., Yugosl.", slide 4987, SMF; *Nilotonia longipora,* male, "Gospic., Yugosl.", slide 4987, SMF; *Nilotonia loricata,* female, [allotype], slide 1758, SMF ; *Nilotonia loricata,* male, slide 1758, SMF; *Nilotonia loricata* [as: *Dartia rostrata*], male, 3693, SMH; *Nilotonia micropora,* [type series], slide xxviii/05, NHB; *Nilotonia micropora,* [type series], slide xxviii/06, NHB; *Nilotonia parva,* male, [type series], slide xxv/74, NHB; *Nilotonia parva,* [type series], slide xxv/75, NMB; *Nilotonia shivai* sp. nov., female, [holotype], "IND` 96/236", CAP; *Nilotonia shivai* sp. nov., male, [allotype], "IND 37/`90", CAP; *Nilotonia pyrenaica,* male, [holotype], slide 4282, SMH; *Nilotonia emarginata,* [holotype], NHP; *Nilotonia emarginata,* [New records], 5 spec. "IND L3/90," 2 spec. "IND L6/90," 1 spec. "IND L8/90," 5 spec. "IND L10/90", 1 spec. "IND L18/90", 1spec. "IND L33/90", 3 spec. "IND `93/2," 2 spec. "IND `93/9," 1spec. "IND `93/21", 1spec. "IND `93/22", 1spec. "IND `93/23", 1spec. "IND `93/26", 1spec. "IND `96/190," 1spec. "IND `96/191," 1spec. "IND `96/222"; specimens in CAP; *Nilotonia rackae,* female, [type], "Sc/Sp 78/104", NMB; *Nilotonia rackae,* female, "Sc/Sp 78/25," NHB *Nilotonia schwoerbeli,* [type series], NMB; *Nilotonia scutata,* male, [paratype], slide 4035, SMH; *Nilotonia thermophila,* male, female, [holotype and allotype], slide 3698, SMH; *Nilotonia violacea,* male, [holotype], slide 3695, SMH; *Nilotonia violacea,* female, [allotype], slide 3696, SMH; *Nilotonia vietsi,* male, female, [type series], NMB
Location of t.g.: SMH?
New synonyms: subgenus *Tadagatonia* Cook, 1967 as syn. of subgenus *Nilotonia* (s.s.)

Definition (adults)

Characters of the Anisitsiellinae as defined above and:
• Sclerotization of the dorsum either with two small postocularia platelets and a posteromedian platelet (Fig. 99), or these platelets enlarged and fused in various ways (e.g., Fig. 3).
• Ventral secondary sclerotization varying from none to extensive sclerotization (Fig. 3); some species with complete ventral shields.
• Chelicera *Dartia*-like (Fig. 102a) or *Nilotonia loricata*-like (Fig. 88a).
• Palpus "anisitsiellid-like"; ventral surface of P2 in several species denticulate.
• IV-L-6 with claws absent or reduced to small setae.

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Dividing *Nilotonia* into two subgenera groups

Comparison between *Nilotonia* (s.s.) *loricata* and *Nilotonia* (*Dartia*) *borneri* reveals a series of differences between the two species.

(1) *N. loricata* is characterized by an extremely elongated chelicera, by a P2 with a ventral surface without denticles, by a P4 with only very small ventral tubercles, by swimming hairs present on the fourth leg, by extensive secondary sclerotization on the ventral side, and by acetabula of ordinary size, without enlarged basal sclerites.

(2) *N. borneri* is characterized by a sexual dimorphism in the shape of the second leg, by a chelicera of ordinary length (as shown in Fig. 95), by a palp in which the ventral surface of P2 is denticulate and the tubercles on P4 are well developed, by the absence of swimming hairs, by the absence of secondary sclerotization, and by the basal sclerites of the acetabula being enlarged, with the two posterior ones fused to each other on each side and carrying acetabula of clearly reduced size.

Despite these many differences between the two species, in my opinion there is currently only one feature that allows us to divide the genus *Nilotonia* in a convincing way into two large groups of subgenera. These are:
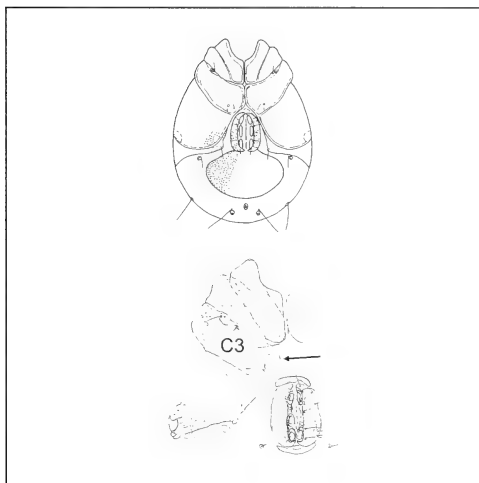
FIG. 86. Ventral view of *Nilotonia* (*s.s.*) *loricata* (top) [Fig. from Lundblad (1941d)]. Right coxal groups and GF of *Nilotonia* (*Dartia*) *boettgeri* (bottom) [original drawing from holotype slide, NHB].

(1) the *Nilotonia*-like subgenera, with medial margins of both C3 and C4 meeting anteriorly from the GF and forming a medial suture line [this type of coxal organization is found in the subgenera *Nilotonia* (s.s.), *N.* (*Mamersonia*) and *N.* (*Manotonia*)], and:

(2) the *Dartia*-like subgenera, with medial margins of C3 only forming a medial edge in the region anterior to the genital field, as given in Fig. 86 [this type of coxal organization is found in the subgenera *N.* (*Dartia*), *N.* (*Dartonia*), *N.* (*Dartiella*) and *N.* (*Tadjikodartia*)].

It is quite possible to characterize several subgenera of *Nilotonia*, as is shown below. However, all characters show different distribution patterns among the 42 species. Hence it does not seem advisable to raise the two subgenera groups to the state of genera.

The *Dartia*-like subgenera include 25 species. They are characterized by the combination of at least 3 of the following 4 characters:

(1) well-developed ventral tubercles on P4 (exceptions: *N.* (*Dartonia*) *rizeensis*, *N.* (*Dartiella*) *fundamentalis*),

(2) P2 with a denticulate ventral surface (present in 19 of 25 species) and/or with ventral seta on P2 situated on a tubercle (present in 5 of 25 species) (exceptions with none of these two characters are: *N.* (*Dartiella*) *catarrhacta*, *N.* (*Dartiella*) *fundamentalis*, *N.* (*Dartonia*) *navina* and *N.* (*Dartonia*) *perplexa*),

(3) IV-L-6 equipped with less than 5 lateral setae (exceptions: some specimens of *N.* (*Tadjikodartia*) *emarginata*),

(4) additional to the lateral setae, the IV-L-6 is equipped in 20 of the 25 species with 1–3 strong, enlarged terminal setae (no exception, but *N. simoni*, assigned to the *Nilotonia*-like subgenera, does possess an elongated terminal seta as well).

The *Nilotonia*-like subgenera include 17 species. They are characterized by:

(1) P4 with ventral tubercles absent or small (exceptions: *N.* (*Manotonia*) *gracilipalpis*, *N.* (*Manotonia*) *musicola*),

(2) P2 never denticulate ventrally and never with ventral seta situated on a tubercle (no exception, but in addition to the *Nilotonia*-like species, 3 *Dartia*-like species show this character combination!), in two species the ventral border of P2 appears waved (*N.* (*Manotonia*) *petri* and *N.* (*Mamersonia*) *simoni*),

(3) IV-L-6 with 5-10 small lateral setae in 12 species (in 6 species less than 5 lateral setae present), IV-L-6 without a long terminal seta (exception: *N.* (*Ma-*

mersonia) *simoni*), IV-L-6 with serrate margin (in 14 of the 17 *Nilotonia*-like species, but a serrate margin is also present in 4 of the Dartia-like species),

(4) secondary sclerotization present ventrally, extent varying from "only at the posterior border of C4" or "large plates" to "ventral shield complete" exception: no secondary sclerotization is found in *N.* (*Manotonia*) *petri*.

The subgenera and species included in *Nilotonia* in this study are arranged in subgenera as shown in the following list. Information on distribution and on collections, in which type material or material for comparison is held, are given as well. The key to the subgenera given below is valid for all currently known species.

(1) *N.* (s.s.) *loricata* (Nordenskiöld, 1905) [Af (Sudan); SMF, SMH]

(2) *N.* (s.s.) *africana* (Daday, 1905) [Af (Rwanda, Bur.); (NMB)]

(3) *N.* (s.s.) *cooki* sp. nov. [As (India); CAP]

(4) *N.* (s.s.) *indica* Walter, 1928 [As (India, Sri Lanka); CNM, CAP]

(5) *N.* (*Mamersonia*) *amazonica* (Viets, 1954) [S-Am (Brazil); SMF]

(6) *N.* (*Mamersonia*) *biscutata* Bader, 1995 [C-Am (Trinidad); NMB]

(7) *N.* (*Mamersonia*) *monoscutata* Bader, 1995 [C-Am (Trinidad); NMB]

(8) *N.* (*Mamersonia*) *similis* Bader, 1995 [C-Am (Trinidad); NMB]

(9) *N.* (*Mamersonia*) *simoni* Org. & Gruia, 1983 [S-Am (Venezuela); ?]

(10) *N.* (*Manotonia*) *gracilipalpis* Lbld., 1942 [Af (Ethiopia); SMH]

(11) *N.* (*Manotonia*) *musicola* (Walter, 1935) [Af (Ivory Coast); ?]

(12) *N.* (*Manotonia*) *shivai* sp. nov. [As (India, Himalayas); NMB]

(13) *N.* (*Manotonia*) *petri* Cook, 1979 [Af (Ghana); CNM]

(14) *N.* (*Manotonia*) *scutata* Cook, 1966 [Af (Cameroon); CNM, SMF]

(15) *N.* (*Manotonia*) *tegulata* (Viets, 1951) [Af (Algeria), Eu (Italy); SMF]

(16) *N.* (*Manotonia*) *testudinata* Cook, 1966 [Af (Liberia) CNM]

(17) *N.* (*Manotonia*) *violacea* Lbld., 1951 [Af (Kenya); SMH]

(18) *N.* (*Dartonia*) *caerulea* (Viets, 1929) [As (Sumatra, Java); SMF]

(19) *N.* (*Dartonia*) *crassipalpis* (Lbld., 1941) [As (Java); SMH]

(20) *N.* (*Dartonia*) *perplexa* Cook, 1967 [As (India); CNM , SMF]

(21) *N.* (*Dartonia*) *rizeensis* (Özkan & Bad., 1988) [As (Turkey); ?]

(22) *N.* (*Tadjikodartia*) *emarginata* (Sok., 1948) [As (Tajikistan, Iran, India); NHP]

(23) *N.* (*Dartia*) *borneri* (Walter, 1922) [Eu (Switzerland, Germany, Netherlands, Romania); NHB]

(24) *N.* (*Dartia*) *harrisi* (Soar, 1917) [Eu (England); London?]

(25) *N.* (*Dartia*) *erzurumiensis* Özkan & Syo., 1989 [As; ?]

(26) *N.* (*Dartia*) *vietsi* Bader & Sepas., 1980 [As (Iran); NMB]

(27) *N.* (*Dartia*) *boettgeri* (Walter, 1925) [As (Iran); NMB]

(28) *N.* (*Dartia*) *turcica* (Özkan & Soy., 1989) [As (Turkey); ?]

(29) *N.* (*Dartiella*) *catarrhacta* (Lbld., 1941) [Af, (South Africa); SMH]

(30) *N.* (*Dartiella*) *fundamentalis* Bader, 1995 [As (Israel); NMB]

(31) *N.* (*Dartiella*) *gallica* Motas & Ang., 1967 [Eu (France); ?]

(32) *N.* (*Dartiella*) *hanniae* Bader, 1995 [As (Israel); NMB]

(33) *N.* (*Dartiella*) *longipora* (Walter, 1925) [Af (Algeria), Eu (Greece, Italy, Spain, Croatia, Poland, USSR) ??; (SMF)]

(34) *N.* (*Dartiella*) *micropora* (Walter, 1939) [Af (Congo, Kivu); NMB]

(35) *N.* (*Dartiella*) *navina* Cook, 1967 [As (India); CNM]

(36) *N.* (*Dartiella*) *ortali* Bader, 1995 [As (Israel); NMB]

(37) *N.* (*Dartiella*) *parva* (Walter, 1931) [Af (Sahara), Eu; NMB]

(38) *N.* (*Dartiella*) *pontifica* Gerecke, 1992 [Eu; CRG]

(39) *N.* (*Dartiella*) *pyrenaica* Lbld., 1956 [Eu (Spain, Italy); CRG]

(40) *N.* (*Dartiella*) *rackae* Bader & Sepas., 1980 [As (Iran); NMB]

(41) *N.* (*Dartiella*) *robusta* (Walter, 1931) [Af (Sahara), As (Israel, Saudi Arab.); NMB, CRG]

(42) *N.* (*Dartiella*) *thermophila* Lbld., 1951 [Af (Congo, Ruwenzori); SMH]

Key to the subgenera of *Nilotonia* (Nordenskiöld, 1905)
(artificial key to adults)

1　In the region anterior to the genital field the medial borders of the third and forth coxae parallel to each other (Fig. 86)
　　. . . . .[*Nilotonia*-like subgenera]　2

1*　In the region anterior to the genital field the third coxae with pointed medial edge (Fig. 86)
　　. . . . .[*Dartia*-like subgenera]　4

2　With swimming hairs distally on IV-L-5 (Fig. 89); dorsum with three platelets of moderate size (Fig. 13) . . . . *Nilotonia* (s.s.)

2*　not so　. 3

3　With clearly elongated thin setae on IV-L-3, IV-L-4 or IV-L-5, but without swimming setae; in most species with extensive secondary sclerotization dorsally . . . . *N. (Mamersonia)*

3*　If larger setae are present distally on segments IV-L-3,4,5 then they are strong not thin; IV-L-6 with only a few or small lateral setae and never with elongated terminal seta; dorsum with posteromedial plate either enlarged as shown in Fig. 95, or of moderate size . . . . *N. (Manotonia)*

4　First coxae extending posteriorly, typically nearly reaching the anterior border of the genital field and IV-L-6 with more than one strong terminal seta (Fig. 100) . . . . *N. (Dartonia)*

4*　not so　. 5

5　Coxoglandulare 4 protruding together with parts of C3 over posterior parts of C2 as shown in Fig. 99　. . . . . *N. (Tadjikodartia)*

5*　not so　. 6

6　Gap between first and second acetabula longer than length of first acetabula, and basal sclerites of acetabula with well visible chitinisation; chitinization of posterior two pairs typically fused on each side; acetabula reduced in size, and in most of the species a sexual dimorphism leads to typically shaped terminal segments in the second pair of legs ("*Dartia*-leg") in males (Fig. 96) . . . . *N. (Dartia)*

6*　Gap between first and second acetabula shorter than length of first acetabula, but typically acetabula extend along the medial border of the genital flaps without gaps; if the acetabula are reduced in size with gaps between them, then the basal sclerites are not, or only partly chitinized . *N. (Dartiella)*

Discussion of subgenera and species

Subgenus: *Nilotonia* (s.s.) Thor, 1905

Type: *Teutonia loricata* Nordenskiöld, 1905. Syn.: *Neodartia* Lundblad, 1952 (K. Viets 1956b). *Tadagatonia* Cook, 1967, nov. syn.

Definition (adults)

Characters of the genus *Nilotonia* and of the *Nilotonia*-like subgenera as defined above and:
- IV-L-5 distally with a row of 3–5 long swimming hairs.
- Chelicera elongated, with Length-to-height ratio above 8 (below 7 in the other members of the genus).
- Dorsum without larger plates, but with the pair of anterior platelets and the single posteromedial platelet typical of the genus.
- Venter with varying extent of secondary sclerotization, from little secondary sclerotization posterior to C4 in the female of *N. indica* to a complete ventral shield in the male of *N. cooki* sp. nov.

Discussion of subgenus *Nilotonia* (s.s.)

The existence of swimming hairs in *Nilotonia* (s.s.) has been ignored in most recent publications. Cook (1974) states that swimming hairs are absent in all
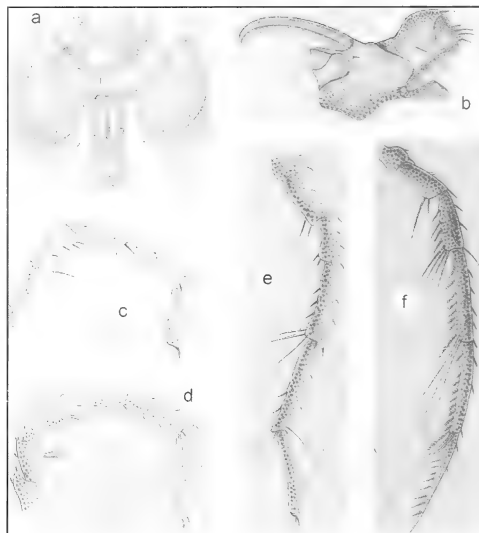
FIG. 87. *Nilotonia* (*s.s.*) *africana* (Daday, 1910): (a) VS, (b) gnathosoma and palps, (c) – (e) legs 1-4, Figs. from Daday (1910).
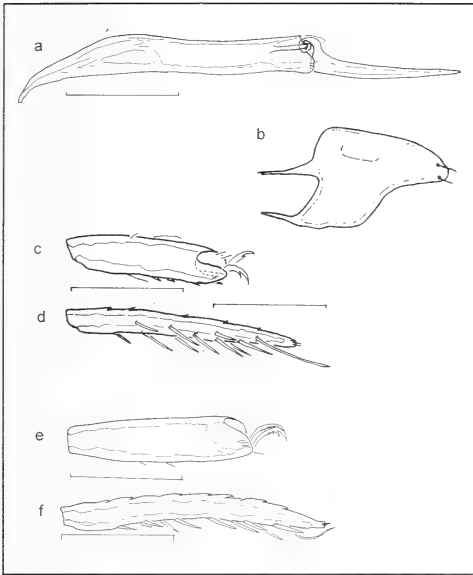
FIG. 88. *Nilotonia loricata*: (a) chelicera, (b) gnathosoma, (c) I-L-6 (male), (d) IV-L-6 (male), (e) I-L-6 (female), (f) IV-L-6 (female). Scale bars = 100 ìm but Fig. (b) not to scale [Fig. a from slide 3699 coll. Lbld. SMH; Fig. b from Lundblad (1951); Figs. c - f from slide 1785 in coll. Viets, SMF].

subgenera in the genus *Nilotonia*, with the exception of *Tadagatonia*.

However, the species *N.* (s.s.) *loricata*, and consequently subgenus *Nilotonia* (s.s.), is characterized by the possession of true swimming hairs as well as by other striking features (see definition). A comparison of *N. loricata* and *N. indica* makes it obvious that on the one hand *Tadagatonia* is a synonym of *Nilotonia* (s.s.), and on the other that most species placed in the subgenus, e.g., in Cook (1974) or Viets (1987), have to be excluded from it.

In all four species assigned to the subgenus in this study, swimming hairs are present on different segments of the third and fourth legs. A row of 3–6 swimming hairs is found at the distal end of segment IV-L-5. In some of the species assigned in this study to *Nilotonia* (*Mamersonia*), there are found some elongated thin setae in similar positions, but none of the *Mamersonia* species shows a row of true swimming hairs at the distal end of segment IV-L-5.

Nilotonia (s.s.) includes two species from Africa and two from the Indian peninsula. *Nilotonia* (s.s.) is most probably the sister group of the subgenus *Ma-*

mersonia (which is known from the Amazon region and Trinidad only).

Nilotonia loricata has been reported from Sudan, Cameroon and Uganda; 5–6 swimming hairs are present distally on IV-L-5 in this species, but only 3 are found in *N. africana*, according to the figures given by Daday (1910). *N. africana* has been commonly treated as a junior synonym to *Nilotonia loricata*. However, comparison of the figures and text of Daday (1910) with material of *Nilotonia* (s.s.) *loricata* shows that there are differences between the two species. For example the postgenitale is much smaller in *N.* (s.s.) *africana*, and on the IV-L-6 the subterminal seta is not slightly larger than the preceding seta. Hence I suggest keeping *N.* (s.s.) *africana* as a valid name, until topotypic material can be compared with the better known *Nilotonia* (s.s.) *loricata*.

N. (s.s.) *cooki* sp. nov. and *N.* (s.s.) *indica* are both found in the Indian peninsula. Apart from the presence of swimming setae they share with the two African species of the subgenus the elongated chelicera and the characteristic shape of the gnathosoma (with an elongated tip).
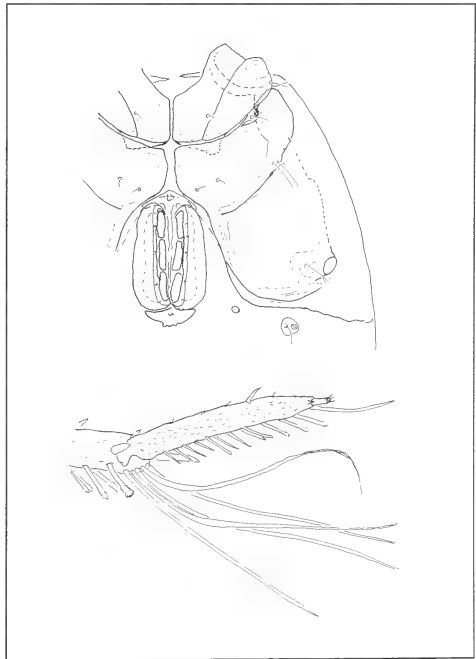
FIG. 89. *Nilotonia indica* Walter, 1928 (female): VS (top), IV-L5,6 (bottom), Figs. from slide IND K36 in coll. CAP.
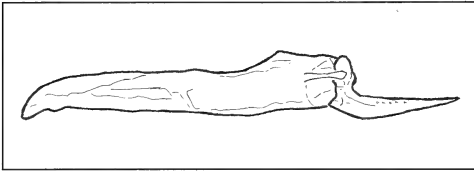
FIG. 90. *Nilotonia indica* Walter, 1928 (male): Chelicera [Fig. from slide Ec3-3-90, 31.12.90].

Walter (1928) based the species *N.* (s.s.) *indica* on nymphs collected in a pond in south India. Cook (1967) assigns adults to this species, which he collected from standing water bodies only 150 kilometers from the locus typicus of *N.* (s.s.) *indica*. However, additional material from India, collected during the course of this study, reveals that the adults described by Cook (1967) belong to a new species. This new species, and the adults assigned in this study to *N.* (s.s.) *indica*, are described below.

Nilotonia indica Walter, 1928

Holotype: (Nymphotype) lost. Further material: Female – described in Gledhill and Wiles, 1997; Male from "coll. IND 25. 09. 90 A" described below. New records: 1 nymph in "IND K 61/2, 28. 11. 89"; 2 males and one nymph in "IND Ec3, 31. 12. 90"; 1 female in "IND -65-"; 1 female in "IND K36"; 3 females in "IND coll –350–"; 2 females in "IND 90-69-PK9: 12. 06. 90"; 2 males and 1 female in "IND 90-69-PK7: 12. 06. 90."

Description of males. The males are similar to the females, described in detail by Gledhill & Wiles (1997). They differ from females mainly in that the postgenitale is slightly larger and the sclerotization is slightly greater.

Discussion. The adults assigned here to the nymphotypus of *N. indica* show a similar extent of secondary sclerotization posterior to the C4 in adult and nymphal stage, and differ in this character from the following species. In the samples collected for this study 15 specimens of *N. indica*, but only 2 specimens of *N. cooki* sp. nov. (described below), were discovered.

Distribution. The species is now known from various places on the Indian peninsula (from Delhi to Trivandrum) and from Sri Lanka.

Habitat. This species, as well as the following one, were found in ponds covered with dense plant carpets. As regular measurements revealed, the concentration of dissolved oxygen was often near zero in these ponds (Panesar 1993).

Nilotonia cooki sp. nov.

Holotype: 1 male – as described by Cook 1967 [pond, 8 miles west of Gundlupet, Mysore State, India; Jan. 10, 1963; collection 51]; Allotype: 1 female from coll. "IND 1990-06-12_2 [69-K8]"; Nymph: 1 nymph from coll. "IND 1990-12-31 [Ec(3)]."

Description of female. The females are similar to the males, described in detail by Cook (1967), in all features except the extent of ventral secondary sclerotization. While in males a complete ventral shield is present, in the females only moderate secondary sclerotization posterior to C4 and a slightly enlarged postgenitale is found.

Discussion. Males of *N.* (s.s.) *cooki* are the only ones of the subgenus in which a complete ventral shield is present. The females, though less sclerotized, have the largest secondary sclerotization posterior to C4. A nymph was found in the material, and tentatively assigned to the species, which was equipped with the typical row of swimming hairs at IV-L-5 and an almost complete secondary sclerotization of the venter.

Distribution. The male was found in a pond near Gundlupet (Mysore state, India) and the female and nymph in a pond near Delhi (Uttar Pradesh, India).

Habitat. See under the preceding species.

Subgenus: *Mamersonia* (Viets, 1954)

Mamersonia Viets, 1954
Mamersonia amazonica Viets, 1954

Definition (adults)

Characters of the *Nilotonia*-like subgenera and:
• Dorsal plates always enlarged, and in two of the five species a complete dorsal shield is present.
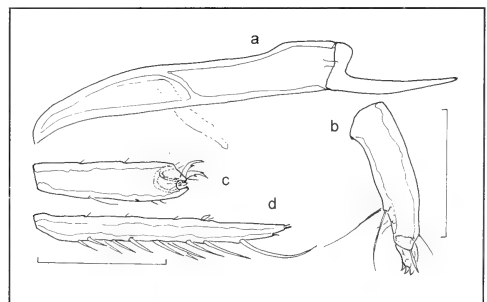
FIG. 91. *Nilotonia (Mamersonia) amazonica*: (a) chelicera, (b) palpus segments 5,6, (c) I-L-6, (d) IV-L-6. Scale bars = 100 μm [all Figs. from slide 7292, coll. Viets, SMF].

- Never with true swimming setae distally on IV-L-5 (a row of elongated stiff, thin setae are present in this position in some species); other segments of legs with elongated thin setae in several species.
- VS with extensive secondary sclerotization in all species, often a small furrow of soft integument is left between the postgenitale and the secondary sclerotization posterior to the genital field.

Species included

Nilotonia (*Mamersonia*) *amazonica* (Viets, 1954) was described from the Amazon river in Brazil, and *N.* (*M.*) *simoni* Orghidan & Grujia, 1983, was discovered in Venezuela. The three other species – *N.* (*M.*) *biscutata*, *N.* (*M.*) *monoscutata* and *N.* (*M.*) *similis* – were all described from collections on Trinidad (Bader 1995). Hence all five species now assigned to this subgenus are found in or around the Amazon region.

    Nilotonia (*Mamersonia*) *amazonica* shares with *Nilotonia* (s.s.) the elongated chelicera and the chaetotaxy of IV-L-6, including the subterminal seta on IV-L-6 being slightly longer than the preceding setae, and the fact that exactly in the positions where the true swimming hairs are located in *Nilotonia* (s.s.) species, enlarged, stiff setae are found in *Nilotonia* (*Mamersonia*) *amazonica*. However, it shares with all other species assigned to the subgenus the absence of true swimming setae, and shares with the three species from Trinidad the enlarged dorsal plates.

    N. (*M.*) *simoni* is the only species in the subgenus with moderate secondary sclerotizations and is the only species in the *Nilotonia*-like subgenera with a clearly elongated terminal seta on IV-L-6. However, it shares with the other species of the subgenus the presence of elongated, stiff setae on segments IV-L-3,4,5.

Subgenus: *Manotonia* (Viets, 1935)

Mania Walter, 1935; Name preoccupied by Hübner, 1816 (Lepidoptera); Type *Mania musicola* Walter, 1935 (Monobasic).
Manotonia Viets, 1935; Type *Mania musicola* Walter, 1935.

Definition (adults)

Characters of the *Nilotonia*-like subgenera and:
- Without elongated, thin setae on IV-L. If elongated setae are present, they are strong and broad.
- IV-L-6 never with elongated terminal or subterminal seta; lateral setae on IV-L-6 typically reduced in number (5-0) and small.
- Sclerotization on dorsum and venter variable.
- Dorsal seta on P1 typically absent.
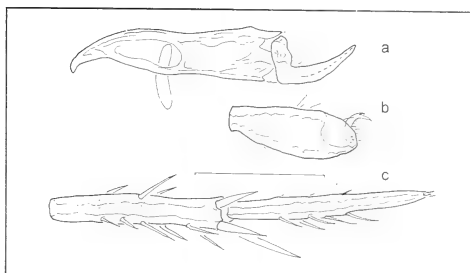
FIG. 93. *Nilotonia* (*Manotonia*) *scutata* (male): (a) chelicera, (b) I-L-6, (c) IV-l-5,6. Figs. a and c from slide 6894 coll. Viets, SMF; Fig. b from paratype slide 4035 coll. Viets, SMF.

Species included

Gerecke (1991) points out that there are no characters to separate the female of *N.* (*M.*) *tegulata* from certain more sclerotized species of *Nilotonia*. Furthermore, Lundblad (1952) depicts for *N.* (*M.*) *gracilipalpis* a genital sclerite which is very similar to that of *N.* (*M.*) *tegulata* (with Brachia distalia of reduced size). Consequently I propose to include this species and several similar ones in *Manotonia* and to reduce *Manotonia* to a subgenus of *Nilotonia*. The species included in the subgenus *Manotonia* in this study are:
(1) *N.* (*Manotonia*) *gracilipalpis* Lbld., 1942; Africa (Ethiopia)
(2) *N.* (*Manotonia*) *musicola* (Walter, 1935); Africa (Ivory Coast)
(3) *N.* (*Manotonia*) *shivai* sp. nov.; Asia (India, Himalayas)
(4) *N.* (*Manotonia*) *petri* Cook, 1979; Africa (Ghana)
(5) *N.* (*Manotonia*) *scutata* Cook, 1966; Africa (Cameroon)
(6) *N.* (*Manotonia*) *tegulata* (Viets, 1951); Africa (Algeria), Eu (Italy)
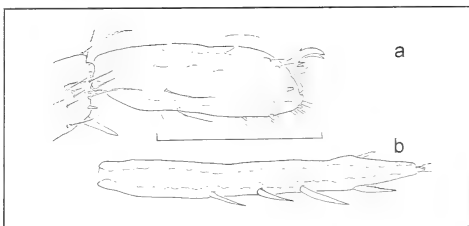
FIG. 92. *Nilotonia* (*Manotonia*) *violacea*: (a) I-L-6, (b) IV-l-6. Fig. a from holotype slide 3695, SMH; Fig. b from paratype slide 3696, SMH.
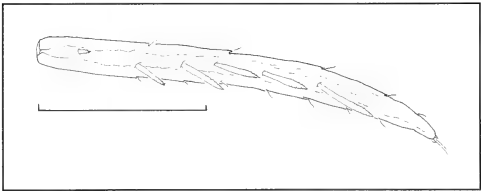
FIG. 94. *Nilotonia* (*Manotonia*) *gracilipalpis*: Leg IV-l-6. Scale bar = 100 μm [Fig. from paratype, slide 3167 SMH].

(7) *N.* (*Manotonia*) *testudinata* (Cook, 1966); Africa (Liberia)

(8) *N.* (*Manotonia*) *violacea* Lbld., 1951; Africa (Kenya)

Distribution. Most species of the subgenus are known from Africa only. *N.* (*M.*) *tegulata* has been reported from Africa as well as from European parts of the Mediterranean region. One new species (described below), assigned to this subgenus in this study, was found in springs and streams in the Himalayas (India, Asia).

Nilotonia (*Manotonia*) *shivai* sp. nov.

Holotype: 1 female adult from collection "1996-06-16[`96/236]" (Naggar-Nala, drift-sample, Kullu Valley, Himachal Pradesh, India). Paratypes: 1 male adult from collection "1990-04-20 [53(2) 37/'90]" (near Gaurikung, road. towards Kedarnath, seepage area, Garhwal Himalayas, Uttar Pradesh, India).
Holotype material placed in the NMB. Paratype will be deposited in the ZSI (India).

TABLE 28. *Nilotonia* (*Manotonia*) *shivai* sp. nov. 1: Idiosoma [measurements in μm].

N. (M.) shivai sp. nov. Holotype Paratype Collection	1996-06-16 ['96/236]	1990-04-20 [53(2);37/90]
sex [m = male; f = female]	f	m
Idiosoma / Dorsal shield		
Idiosoma: length	670	-
Ventral length (incl. C1)	720	-
Idiosoma: max. width	590	-
Dorsal shield: length	610	600
Dorsal shield: width	463	442
DS: length/width ratio	1,32	1,36
Coxae		
distance: gnathosoma – GF	232	230
left to right width C3	350	340
left - right dist. Cg4	103	96
distance: posterior border GF to end of	250	-
distance: posterior border GF to border of sclerotization posterior to C4	10	0
Genital field (GF)		
GF to end of body	250	-
genital opening: width	122	110
genital flaps: length	175	150
genital opening: length/width ratio	1,43	1,36
length of 1st, 2nd and 3rd acetabulum	60 / 55 / 45	55 / 50 / 38
postgenital plate: medial length	60	104
postgenital plate: max. width	162	243
Chelicera		
basal segment; length	207	189
basal segment: height	48	52
basal segment.: length/height ratio	4,3	3,6
claw: length	77	71
claw: height	36	40
claw: length/height ratio	2,1	1,8
total length of chelicera	284	260

TABLE 29. *Nilotonia* (*Manotonia*) *shivai* sp. nov. 2: Palpal data [measurements in μm].

N. (*M.*) *shivai* sp. nov. Collection sex [m=male; f=female]	Holotype 1996-06-16 ['96/236] f		Paratype 1990-04-20 [53(2);37/90] m	
Palpal segments	left palp	right palp	left palp	right palp
P1-length	30	35	28	30
P1-height	47	46	49	45
P1-length/height ratio	0.64	0.76	0.57	0.67
P1: % of total length	7.5	8.5	7.7	8.1
P2-length	125	125	109	115
P2-height	67	68	63	64
P2-length/height ratio	1.87	1.84	1.73	1.80
P2: % of total length	31.4	30.5	29.9	31.1
P3-length	70	75	65	64
P3-height	50	50	46	47
P3-length/height ratio	1.40	1.50	1.41	1.36
P3: % of total length	17.6	18.3	17.8	17.3
P4-length	141	142	128	127
P4-height (incl. hook)	42	38	33	33
P4-length/height ratio	3.36	3.74	3.88	3.85
P4: % of total length	35.4	34.6	35.1	34.3
P5-length	32	33	35	34
P5-height	17	20	18	18
P5-length/height ratio	1.88	1.65	1.94	1.89
P5: % of total length	8.0	8.0	9.6	9.2
Palpus: total length	398	410	365	370
length ratio P2/P4	3.9	3.8	3.1	3.4

Description of female. (Fig. 95): With characters of the subgenus *Manotonia*. All measurements for the different specimens are given in tables "*N. shivai-*measurements.*" A single large dorsal shield is present. Fused to this shield are found the postocular setae (R2) and two pairs of glandularia. Venter with moderate secondary sclerotization posterior to the fourth coxae and with a slightly enlarged postgenitale. Excretory pore slit-like and without secondary sclerotizations.
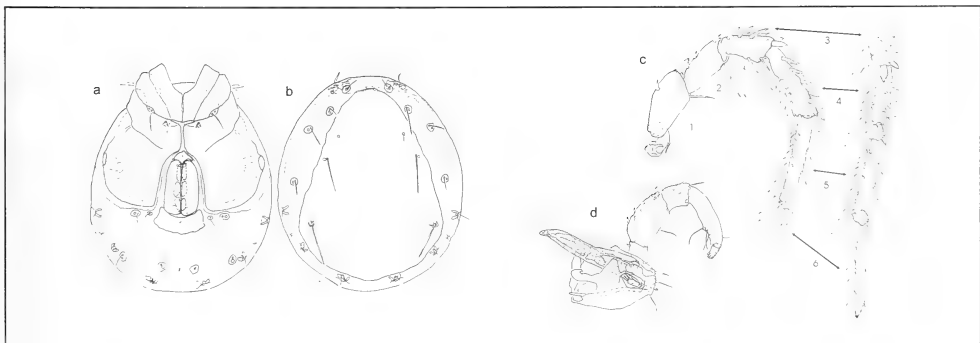
FIG. 95. *Nilotonia* (*Manotonia*) *shivai* sp. nov. (female): (a) VS, (b) DS, (c) IV-L (left and right leg from different views), (d) gnathosoma, chelicera, palp. Figs. a, b from slide IND 1990-04-20_2, Figs. c, d from IND 1996-06-16 (`96/236).

Medial sutures of C3 parallel to each other in the region anterior to the genital field. Cg4 situated posterior to suture C2/C3 and slightly lateral to the point at which suture C1/C2 joins anterior border of C3.

Eye-lenses below the soft integument and both oval in shape.

Anterior end of genital flaps at level of insertions of IV-L. Posterior border of C4 at same level as posterior end of genital flaps.

P1 with dorsal seta present, P2 with 6 dorsal and a long thin ventral seta, P3 with 3 setae, P4 with ventral tubercles small, P5 with small claws.

Basal segment of chelicera without strong dorsal elevation.

Fourth leg as shown in Fig. 95. Claws on anterior three pairs of legs simple and hook-like, with ventral and dorsal clawlet. Dorsal length [μm] of segments 1–6 of IV-L are: 120/100/100/145/185/170 (left leg) and 125/103/100/151/185/lost (right leg). *Description of male*. Similar to female, but with more extensive secondary sclerotization posterior to the fourth coxae and on the postgenital plate. Dorsal length [μm] of segments 1–6 of IV-L are: 120/105/100/140/178/172 (left leg) and 115/100/98/140/176 (right leg).

Nymphs and larvae. Unknown.

Derivatio nominis. With reference to the Indian deity Shiva, who spread his hair to form the Himalayas and in this way rescued the world from being destroyed by the furious goddess Ganga.

Distribution. Known from two locations in the southwestern Himalayas. One is the type locality in the Kullu Valley (upper catchment area of the Beas river) and one from the Garhwal Himalayas near Gaurikund (upper catchment area of river Ganga).

Subgenus: *Dartia* Soar, 1917

Type *Dartia harrisi* Soar, 1917

Definition (adults)

Characters of the genus *Nilotonia* and of the *Dartia*-like subgenera as described above and:

- Gap between first and second acetabulum larger or about as long as first acetabulum. Basal sclerites of acetabula always enlarged and typically the posterior two pairs on each side fused to each other; acetabula always reduced in size.
- With sexual dimorphism expressed in the fifth segment of the second leg in all but one species of the subgenus. This segment is broad and of typical shape and chaetotaxy (as given in Fig. 96) in males and unmodified in females.
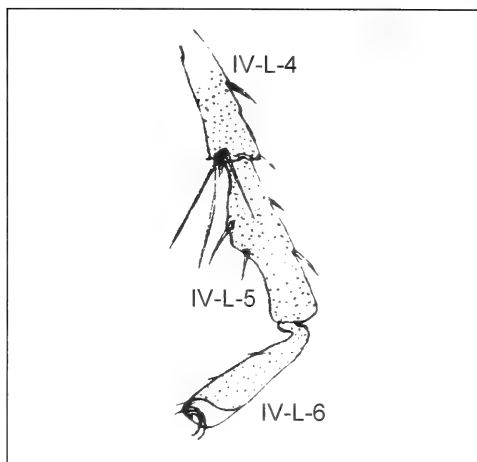
FIG. 96. *Nilotonia* (*Dartia*) *harrisi* Soar,1917: Terminal segments (IV-L-4,5,6) of second leg of the male, the so-called "Dartia-leg."

Species included

The subgenus *Dartia* is commonly defined by the sexual dimorphism in the fifth segment of the second leg. However, the subgenus shows drastic modifications in the genital field, such as (1) gap between first and second acetabulum being larger or about as long as first acetabulum, (2) basal sclerites of acetabula enlarged and posterior two pairs on each side typically fused to each other, and (3) acetabula reduced in size. As pointed out in the general discussion, these modi-
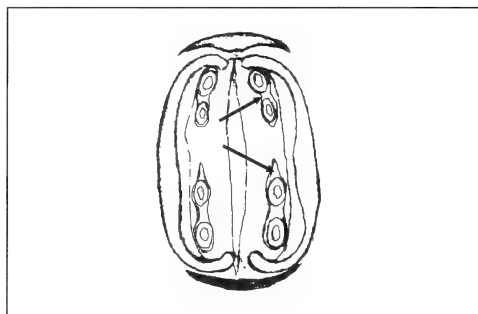
FIG. 97. *Nilotonia* (*Dartia*) *harrisi*: The genital field of *N. D. harrisi* is unique in the proliferation of the first pair of acetabula, leading to a total of four pairs. Note: Arrows indicate the enlarged and fused portions of the ring sclerites of the acetabula. Figs. from Soar (1926).

FIG. 98. *Nilotonia (Dartia) boettgeri* (female, holotype): Shape of right coxae and genital field. Note: On each side the enlarged basal sclerites of the acetabula (indicated on the right side by gray shading) are fused to each other. Fig. from holotype slide, NHB.

fications in the genital field of *Dartia* can be considered as a model for the transformation series connecting Anisitsiellinae and Limnesiinae, leading to the fusion and incorporation of the acetabula into the genital flaps in the latter. The modifications in the genital field of the subgenus *Dartia*, and the characters shared by larvae of *Nilotonia*-species and *Limnesia*, form the major arguments for the placement of the Anisitsiellinae in the family Limnesiidae in this study.

The following 6 species are included in the subgenus in this study:

(1) *N.(Dartia) borneri* (Walter, 1922); Europe (Switzerland, Germany, Netherlands, Romania)
(2) *N.(Dartia) harrisi* (Soar, 1917); Europe (England)
(3) *N. (Dartia) erzurumiensis* Özkan & Syozal, 1989; Asia
(4) *N.(Dartia) vietsi* Bader & Sepas.,1980; Asia (Iran)
(5) *N. (Dartia) boettgeri* (Walter, 1925); Asia (Iran)
(6) *N. (Dartia) turcica* (Özkan & Syozal, 1989); Asia (Turkey)

Contrary to the common practice, I propose to include all species into the subgenus which show the above specified modifications in the genital field.

Consequently the two species *N.(D.) turcica* and *N. (D.) boettgeri* are assigned to the subgenus *Dartia* in this study. They share the modifications in the genital field and several other characters with the other members of the subgenus. However, *N. (D.) boettgeri* is known only in the female and in *N. (D.) turcica* the males do not express sexual dimorphism.

Subgenus: *Tadjikodartia* Bader, 1980

Type: *Dartia emarginata* Sokolow, 1948
N. schwoerbeli Bader & Sepas., 1979 = *N. emarginata* [syn. nov.]

Definition (adults)

Characters of the genus *Nilotonia* and of the *Dartia*-like subgenera and:
• With Cg4 and parts of C3 protruding over C2.

Species included

Bader mistakes the aberrant leg of *N. (T.) emarginata* depicted in Sokolow (1948) as a modification, similar to the modified II-L-5,6 found in males of *Dartia*.
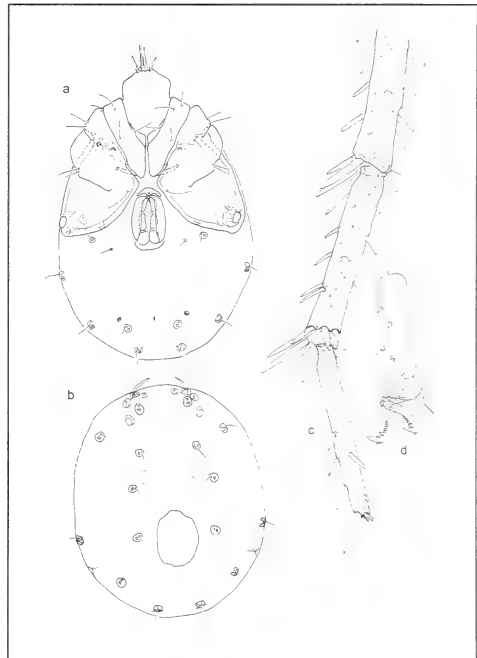
FIG. 99. *Nilotonia (Tadjikodartia) emarginata* (female): (a) VS, (b) DS, (c) IV-L-4,5,6, (d) III-L-6. Figs. from slide IND `96/191.

However, Sokolow (1948) points out that only the leg on one side is unusual, while the respective leg on the opposite site is of ordinary shape.

Still, I suggest keeping this subgenus as valid for the type species that differs from all remaining *Nilotonia* species in having the Cg4 and parts of C3 protrude over C2.

The new material from the Himalayas, and investigations on the holotype of *N. (T.) emarginata*, suggest that *N. schwoerbeli* Bader & Sepasgozarian, 1979, is a junior synonym to *N. (T.) emarginata*.

Hence, the subgenus includes a single species *N. (Tadjikodartia) emarginata* (Sokolow, 1948), which is widespread from the Iran and Tajikistan up to the Indian Himalayas.

Subgenus: *Dartonia* Viets, 1929

Type: *Dartia caerulea* Viets, 1929
Syn.: *Dartoniella* Lundblad, 1941 (K. Viets 1956b)

Definition (adults)

Characters of the genus *Nilotonia* and of the *Dartia*-like subgenera and:
- With more than one strong terminal seta present on IV-L-6.
- Without a gap between first and second pair of acetabula.
- Typically with medial suture C1/C1 of about the same length as genital flaps (but not so, and suture shorter, in the females of *N. D. perplexa*).

Species included

The subgenus *Dartonia* is easily separated from the other subgenera as it shares several striking characters, such as (1) IV-L-6 terminally with more than one robust seta, (2) either palpus with short and stocky seg-

FIG. 100. *Nilotonia (Dartonia) perplexa*: VS (top), IV-L-6 (bottom). Fig. from Cook (1967).

ments and with P2 dorsally with more than 8 setae or ventral seta peg-like, (3) in males the suture C1/C1 is longer than are the genital flaps and the posterior end of the coxae nearly touches the praegenital plate, and (4) the claws on III-L-6 have strong ventral and/or dorsal clawlets leading to a bidentate or tridentate appearance. Four species from Asia are included in the subgenus in this study:

(1) *N. (Dartonia) caerulea* (Viets, 1929); As (Sumatra, Java)
(2) *N. (Dartonia) crassipalpis* (Lbld., 1941); As (Java)
(3) *N. (Dartonia) perplexa* Cook, 1967; As (India)
(4) *N. (Dartonia) rizeensis* (Özkan & Bader, 1988); As (Turkey)

I have excluded *Nilotonia navina* from this subgenus and shifted it to *Dartiella* (see below), as there is only one strong seta present terminally on IV-L-6 and the preceding seta is comparatively thin. Its shape is typical of the lateral setae found in many species of the genus *Nilotonia* on IV-L-6.

Subgenus: *Dartiella* Viets, 1929

Type: *Dartia longipora* Walter, 1925.
N. buettikeri Bader, 1980 = *N. robusta* (Walter, 1931) [syn. nov.]

Definition (adults)

Characters of the *Dartia*-like subgenera as described above and:
- With length of medial suture C1/C1 typically shorter than the genital flaps. With Cg4 situated posterior to suture C2/C3; with no part of C3 protruding over C2.
- Without or with one (but never with more than one) strong elongated seta on IV-L-6.
- In 13 of the 14 species the acetabula extend along the medial border of the genital flaps without gaps; if a gap between first and second acetabulum is present, than it is shorter than the length of first acetabulum (Fig. 102b); in one species (*N.(D.) micropora*) the acetabula are drastically reduced in size and there are large gaps between them, however the basal sclerites are not, or only slightly chitinized in this species.

Species included

Gerecke & Smith (1993) described the larvae of *N. (D.) longipora*, which shows a character combination relating it strongly not only to *Nilotonia (Manotonia) tegulata* and to the genus *Anisitsiella*, but also to the
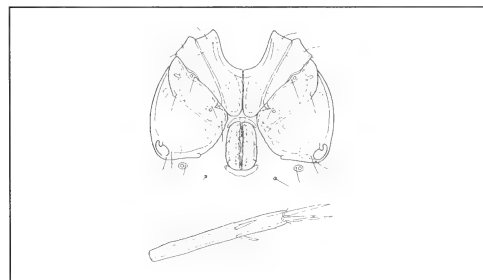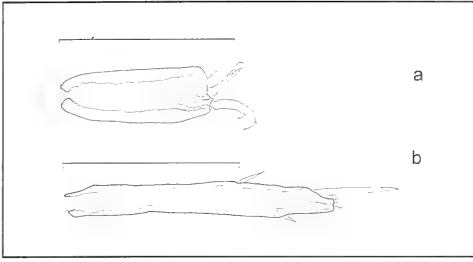
FIG. 101. *Nilotonia* (*D.*) *catarrhacta* (Lundblad, 1941): (a) I-L-6, (b) IV-L-6. Scale bars = 100 μm.

genus *Limnesia* (see discussion of larvae under "Limnesiidae").

In the subgenus *Dartiella* 14 species are united. This subgenus is an assemblage of species that do not fit in the better-defined neighboring subgenera. While in *N.* (*D.*) *micropora* the acetabula are drastically reduced in size (with large gaps between them and without any sign of chitinized basal sclerites), in all other members the acetabula extend along the genital opening with only small gaps between them. However in several species (e.g., *N.* (*D.*) *longipora*) the basal sclerites carrying the acetabula are well chitinized.

(1) *N.* (*Dartiella*) *catarrhacta* (Lbld., 1941); Africa, (South Africa)
(2) *N.* (*D.*) *fundamentalis* Bader, 1995); Asia (Israel)
(3) *N.* (*D.*) *gallica* Motas & Ang., 1967; Europe (France)

(4) *N.* (*D.*) *hanniae* Bader, 1995; Asia (Israel)
(5) *N.* (*D.*) *longipora* (Walter, 1925); Africa (Algeria), Europe (Greece, Italy, Spain, Croatia, Poland, USSR)
(6) *N.* (*D.*) *micropora* (Walter, 1939); Africa (Congo, Kivu)
(7) *N.* (*D.*) *navina* Cook, 1967; Asia (India)
(8) *N.* (*D.*) *ortali* Bader, 1995; Asia (Israel)
(9) *N.* (*D.*) *parva* (Walter, 1931); Africa (Sahara), Europe
(10) *N.* (*D.*) *pontifica* Gerecke, 1992; Europe
(11) *N.* (*D.*) *pyrenaica* Lbld., 1956; Europe (Spain, Italy)
(12) *N.* (*D.*) *rackae* Bader & Sepas., 1980; Asia, (Iran)
(13) *N.* (*D.*) *robusta* (Walter, 1931); Africa (Sahara), Asia (Israel, Saudi Arabia)
(14) *N.* (*D.*) *thermophila* Lbld., 1951; Africa (Congo, Ruwenzori)

N. buettikeri Bader, 1980 = *N. robusta* (Walter, 1931)

Investigation of the holotype of *N. buettikeri* revealed that the "ventral platelet posterior to the genital field" referred to by Bader (1980) is not a chitinized platelet, but an egg. As no other differences between *N. buettikeri* and *N.* (*Dartiella*) *robusta* were found, *N. buettikeri* is suggested as junior synonym to *N.* (*Dartiella*) *robusta* here.

FIG. 102. *Nilotonia* (*Dartiella*) *pyrenaica* Lundblad, 1956: (a) chelicera, (b) genital field. Scale bars = 100 μm.
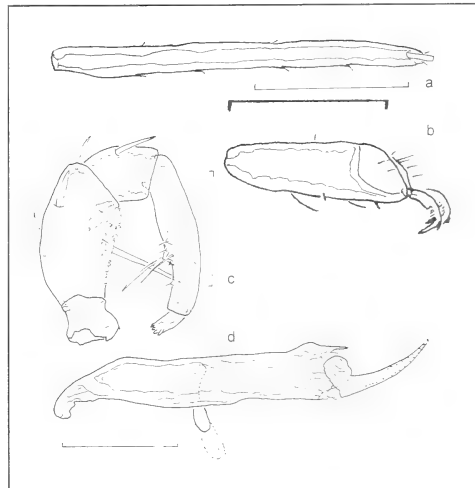
FIG. 103. *Nilotonia* (*Dartiella*) *robusta*: (a) palpus, (b) chelicera, (c) I-L-6, (d) IV-L-6. Scale bars = 100 μm.

Nilotonia (*Dartiella*) *fundamentalis* Bader, 1995

Since the male assigned to this species by Bader (1995) turned out to belong to *N.* (*Manotonia*) *tegulata*, the holotype female is described in some detail and compared to the figure and text of Bader (1995).

Material examined: *Nilotonia fundamentalis* Bader, 1995, ♀, holotype.
Information on slide: "Golan, Meskus 24. 8. 1986; coll. ORTAL 66; Holotypus."
Condition: The holotype specimen is preserved in HOYER, the coxae partly destroyed during preparation; gnathosoma and chelicera broken and partly lost.
Location: NMB.

Inventory (adult, females only)

DS. Posteromedian platelet and pair of anterolateral platelets in size as depicted by Bader (1995: 12, figure 2b). However a "region F", as indicated in that figure, was not visible in the holotype slide.
VS. Contra Bader (1995: 12, figure 2), without extensive secondary sclerotization posterior to C4 or GF. Excretory pore slit-like and without secondary sclerotization. Glandularia of the ventral side slightly enlarged.
Eyes. Eyes-lenses oval in shape (not elongated as depicted in Bader (1995: 12, figure 2)).
Coxae. Coxae in four groups. First coxae medially completely separate, (between them there is possibly a very weakly developed secondary sclerotization present below the integument). C2 and C3 medially separate but laterally adpressed to each other. Suture C3/C4 complete, but medially only weakly expressed and bifurcated, with one part pointing anteriorly.
Cg4. Cg4 situated on C3, medially to the bifurcation.
GF. GF at level of insertions of IV-L.
Ac. Three pairs of Ac of equal size, no gap between first, second and third Ac.
I-L-6. Claws on I-L-6 hook-like and with a dorsal clawlet. I-L-6 without setae, but with one dorsal and a few lateral hairs.
IV-L-6. IV-L-6 with four lateral setae, without elongated terminal seta, with claws reduced to small spines and with several hairs on the terminal part. Shape similar to the IV-L-6 of *N. parva* and *N. boettgeri*.
Palpus. "Anisitsiellid-like" palpus; P1 without dorsal seta, P2 without ventral denticels, ventral seta of medium size, five dorsal setae, P3 with two dorsal and two lateral setae, P4 with a pair of small ventral tubercles and four ventral setae, P5 short.
Chelicerae. destroyed.

Taxonomic placement

Nilotonia fundamentalis Bader, 1995 belongs to the *Dartia*-like subgenera, according to the organization of the coxae (C3 medially forming an edge). It differs from most other species of this group in the comparatively small tubercles on the ventral side of P4, in the absence of denticles on the ventral side of P2, and in the absence of an elongated terminal seta on IV-L-6. I propose to place it next to *N.* (*Dartiella*) *parva* and *N.* (*D.*) *pyrenaica*, with reference to the chaetotaxy of the IV-L-6 and to the acetabula (without larger gaps between them). *N. fundamentalis* differs from these two species in the absence of a ventral series of clawlets on the claws of the anterior legs. Only females of this species are known to science at present. The specimens suspected as males by Bader (1995) belong to *N.* (*Manotonia*) *tegulata*.

Nilotonia (*Dartiella*) *thermophila*

Investigations on the type series of *Nilotonia* (*Dartiella*) *thermophila* Lundblad, 1951 revealed (1) the terminal seta on the IV-L-6 is not absent but lost (this is obvious, as the large insertion is well visible and indicated by an arrow in Fig. 104c), (2) while the acetabula in the holotype male are of ordinary size and number, and without larger gaps between them, in the allotype female they are slightly smaller, and the third acetabulum is divided in 2–3 smaller ones as shown in the following figure.
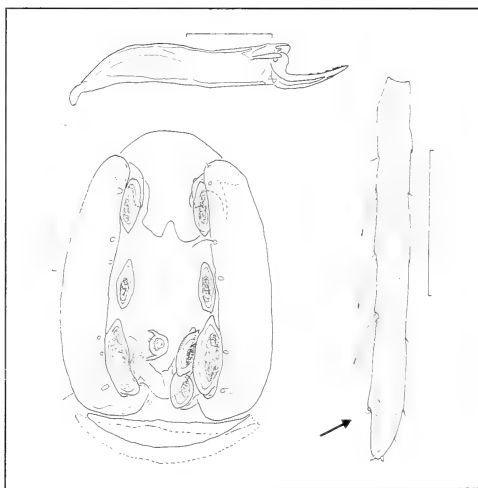
FIG. 104. *Nilotonia* (*Dartiella*) *thermophila* (female, allotype, slide 3698, SNH): (a) chelicera, (b) genital field, (c) IV-L-6 (arrow indicates position of lost seta). Scale bars = 100 μm.

Taxa incertae sedis

The genera *Ranautonia, Stygomamersopsis, Psammotorrenticola* and *Sigthoria* all express characters that suggest they might be placed more appropriatley in other taxa. In the case of *Ranautonia*, information on nymphs or larvae is necessary to draw conclusions about its placement. In the cases of the other three genera classed as "incertae sedis", a revision of the respective Limnesiidae subfamilies would probably produce the information to confirm their placement. However, until such information is available I suggest keeping them tentatively with the Anisitsiellinae.

Genus: *Ranautonia* Viets, 1929 [1 sp.]

Typus generis: *Ranautonia dentipalpis* Viets, 1929. Material examined: *Ranautonia dentipalpis* holotype, slide 4048, SMF. Location of type: SMF.

Definition (adults)

Characters of the Anisitsiellinae as defined above and:
- Chitinization of palps, legs and coxae with a hexagonal structure as in Bandakiopsidae.
- Palpus similar to palp of *Cookacarus*; P5 with long claws, P4 swollen, P2 with ventral seta large and shifted to a distomedial position.
- I-L-6 with claws hook-like.
- IV-L-6 with claws absent or reduced to small setae.

Species included

Ranautonia dentipalpis Viets, 1929 was described from a single male, discovered in a seepage area near the outlet of Lake Ranau (Indonesia).

Inventory (adult, male only)

DS/VS. Dorsally with three small platelets as in Fig. 105. Venter without secondary sclerotization.
Eyes. Eye-lenses of about equal size and the medial and lateral lenses 8 µm apart from each other.
Coxae. Coxae in four groups. Furrows between C2 - C3 and C1 - C1 narrow. Suture C3/C4 incomplete. Insertions of IV-L with well-developed condyles.
Cg4. Cg4 is situated medial to the suture C3/C4.
GF. GF between posterior coxal groups. The posterior of the GF at level of insertions of IV-L.
Ac. Three pairs of Ac of equal size and following one another closely.
I-L-6. I-L-6 with simple hook-like claws.
IV-L-6. With claws reduced and with 5-6 small medial setae. Without swimming hairs.
Palpus. See definition.
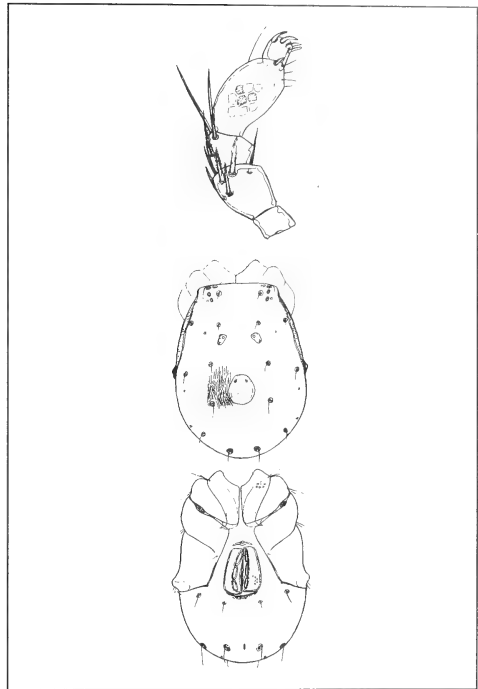
FIG. 105. *Ranautonia dentipalpis* Viets, 1929: Palpus (top), dorsal view (middle), ventral view (bottom). Figs. from Viets (1935).

Chelicerae. The chelicera is very thin and was destroyed during slide-making (Viets 1935). The figure of the gnathosoma drawn by Viets (1935) is given below, along with a sketch of the broken chelicera as it is found now in the holotype slide (Fig. 107).

Taxonomic placement

Ranautonia is tentatively assigned to the Anisitsiellinae here for it shares several characters with the *Nilotonia*-like genera, such as (1) its type of coxal organ-
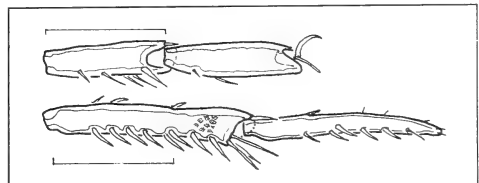
FIG. 106. *Ranautonia dentipalpis*: I-L-5,6 (top), IV-L-5,6 (bottom). Scale bars = 100 µm.
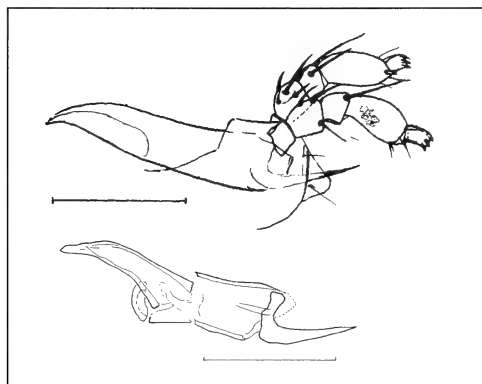
FIG. 107. *Ranautonia dentipalpis*: Chelicera, gnatho-soma and palpi (top). [from Viets (1935)]. Broken chelicera (bottom). Scale bars = 100 µm. Original drawing from slide 4048, SMF.

ization, (2) its type of IV-L, and (3) the shape of the chelicerae.

However, other characters such as (1) the hexagonal structure found in some portions of the chitinized parts, and (2) the shape and chaetotaxy of the palp indicate that *Ranautonia* could be a soft bodied member of the Bandakiopsiidae (with a convergently modified IV-L-6). Information on the larva, or at least on nymphs, would be needed to confirm its placement in one of the two taxa. Yet the genus has not been recorded again since its discovery in 1929.

Genus: *Sigthoria* Koenike, 1907 [1 sp.]

Typus generis: *Sigthoria nilotica* (Nordenskiöld, 1905); preoccupied name: *Amasis niloticus* Nordenskiöld, 1905; nom. nov.: *Sigthoria nilotica* suggested by Koenike (1907). Location of genotype: lost. No material examined.

Definition (adults)

Characters of the Anisitsiellinae as defined above and:
- GF with movable genital flaps and with two rows of usually 12–17 small acetabula present; GF at level of insertions of IV-L.
- Cg4 large and situated near middle of the +/– rectangular C4.
- Claw on I-L-6 hook-like and, according to Lundblad (1969), ventrally with a series of fine setae.
- IV-L-6 with swimming hairs and without well-developed claws; insertions of IV-L with condyles.
- Chelicerae of the *Dartia* type; basal segment without prominent dorsal elevation; proximal end bent ventrally.

Species included

Sigthoria nilotica (Nordenskiöld, 1905) was discovered in samples from the White Nile (Sudan) and has thereafter been reported from several other locations in Africa (Ghana, Liberia, Kenya, Uganda), Asia (Burma, India), and Australia. A second species, *S. minima* (Piersig 1906) was described from standing waters in Asia (Java, Sumatra). Lundblad (1969) compared material from Java, Sumatra and Burma and suggests synonymizing the two species. However, according to the information given by various author's on specimens from different locations, there seem to be several differences that are difficult to interpret. For example: (1) the suture C1/C1 is present in some drawings and absent in others, and (2) the sculpturing of the dorsal shield varies in its shape between species and/or specimens as shown in Fig. 109 Harvey (1990) describes the nymphal stage.
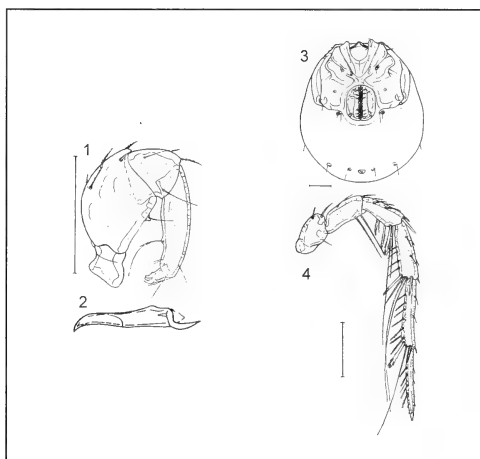
FIG. 108. *Sigthoria nilotica* Nordenskiöld, 1905: (1) palpus, (2) chelicera, (3) VS, (4) IV-L-6. Scale bars = 100 µm. Figs. 1, 3 and 4 from Viets (1935); Fig. 2 from Lundblad (1951).

Inventory (adults)

DS/VS. DS/VS complete. Dorsum with varying sculpturing as shown in Fig. 109.

Eyes. Lateral eyes incorporated into the ventral shield (Cook 1974).

Coxae. In some specimens C1/C1 medially fused and suture absent, in others present.

Cg4. See definition.
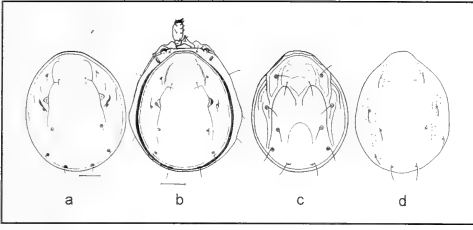
FIG. 109. *Sigthoria nilotica*: (a) and (b) DS (Asia), (c) DS (Africa), (d) DS (Australia). The sculpturing in the dorsal shield of *S. nilotica* either varies, or has been interpreted in various ways in the drawings. Scale bars = 100 μm [Figs. a, b from Viets (1935); Fig. c from Cook (1966); Fig. d from Harvey (1990)].

GF. Genital flaps not boat-shaped (as in *Rheolimnesia* males).
Ac. See definition.
I-L-6. See definition.
IV-L-6. See definition.
Palpus. "Anisitsiellid-like" palpus with ventral seta on P2 arising from a short tubercle and hair-like, P3 with two dorsal and one ventrodistal seta, P4 with small ventral tubercles and 4 hairs, P5 with claws small.
Chelicerae. See definition.

Taxonomic placement

Sigthoria differs from the "anisitiellid-like" mites mainly (1) in the apomorphic proliferation of the acetabula (though, such proliferation has taken place several times in phylogenetically unrelated clades of the Hydrachnellae), and (2) in the position of Cg4 in the middle of C4 (Cg4 is found in a similar position in
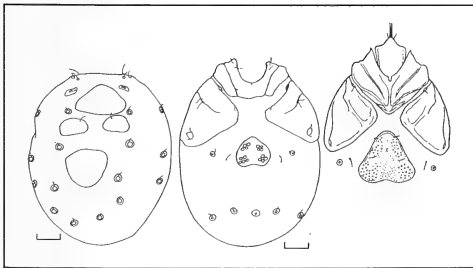
Teutoniidae). The males of the two genera *Rheolimnesia* and *Siboneyacarus*, both placed in the subfamily Protolimnesiinae, share with *Sigthoria* several characters, such as (1) the organization type of the coxae, especially regarding the shape of C4, (2) the palp with P2 bearing the ventral setae on a short tubercle, and (3) rows of (proliferated) acetabula below the movable genital flaps. The two genera differ from *Sigthoria* in characters such as (1) the reduction of the Cg4 or (2) the presence of well-developed claws on IV-L-6.

Gerecke (1995) describes a male of a *Rheolimnesia* species (for synonymy see Goldschmidt, 2001) with a sculpturing of the dorsal shield similar to that of *S. nilotica*, but less prominent. While *Sigthoria* is known from Africa, Asia, and Australia, *Rheolimnesia* and *Siboneyacarus* are restricted to Central and South America. Hence distributional data and adult morphology would allow an interpretation *Sigthoria* as a taxon that was early geographically separated from, but phylogenetically closely related to *Rheolimnesia* and *Siboneyacarus*. As the knowledge of larval stages or of further nymphal stages is necessary to decide on the placement of *Sigthoria*, it is here tentatively kept as genus "incertae sedis" with the Anisitsiellinae.

Genus: *Stygomamersopsis* Cook, 1974 [2 spp.]

Typus generis: *Stygomamersopsis viedmai* Cook 1974. Material examined: *S. anisitsipalpis* female, paratype, slide 6069, SMF; *S. anisitsipalpis*, male, paratype, slide 6070, SMF. Location of types: Holotypes: CNM

Definition (adults)

Characters of the Anisitsiellinae as defined above and:
- Dorsal shields completely covering dorsum, but separated into an anterior and a posterior shield and 6 pairs of lateral platelets.
- Palpus with characteristic chaetotaxy: a row of 4 laterodorsal setae, of which 3 are situated on P2 and one is found on P3. Palpus otherwise "anisitsiellid-like" or "mamersopsid-like." Ventral seta on P2 small or absent, two ventral tubercles on P4 minute and carrying one hair each, claws on P5 small and fused (Fig. 113).
- C4 large and with a long medial suture line C4/C4. Insertions of IV-L with a sclerotized internal socket and situated close to the GF in lateral or anterolateral position.
- IV-L stocky with IV-L-3 and IV-L-4 +/– triangular if seen in lateral view. IV-L-1 constricted and abruptly bent proximally; IV-L-6 with claws reduced.

FIG. 110. Nymphal stages of *Sigthoria nilotoca* and *Rheolimnesia tronchoni*: (A) DS (*S. nilotoca*), (B) VS (*S. nilotoca*), (C) VS (*R. tronchoni*). Scale bars = 100 μm.
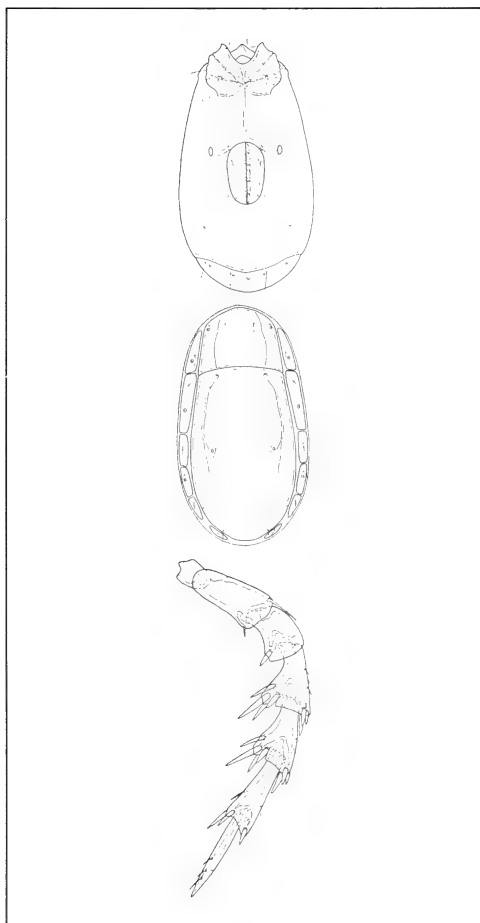
FIG. 111. *Stygomamersopsis anisitsipalpis* Cook, 1974 (female): dorsal shield (top), ventral shield (middle), IV-L (bottom). Figs. from Cook (1974).

Species included

Stygomamersopsis viedmai Cook, 1974 and *Stygomamersopsis anisitsipalpis* Cook, 1974 were both reported from interstitial waters of streams in Spain.

Inventory (adults)

DS/VS. DS and VS complete. For DS see definition.
Eyes. Eye-lenses fused to the ventral shield or absent.
Coxae. A well-developed gnathosomal bay is present between the first coxae. All coxae are fused to the ventral shield. The first three pairs of coxae are confined to a comparatively small anterior area. C4 as described in definition above.

Cg4. Cg4 situated close to midline posterior to suture C2/C3.
GF. Genital flaps more gradually tapering anteriorly in the male.
Ac. Three pairs of Ac of equal size, no gap between first, second and third Ac.
I-L-6. Not described.
IV-L-6. See definition.
Palpus. See definition.
Chelicerae. Basal segment of chelicera with convex dorsal border; cheliceral claw slender (see figure on next page).
Genital skeleton. Investigation of paratype material of *S. anisitsipalpis* (Präp. 6070 in coll. K.O.Viets, SMF) revealed that the genital skeleton is of extraordinary size in this species, reaching about half the length of the body (Fig. 112).

Taxonomic placement

Smith & Cook (1994) point out that the chaetotaxy of the palp, and the organization form of the dorsal and ventral shields, is of the same type in *Stygomamersopsis* and in *Meramecia*, a genus currently placed in the subfamily Neomamersinae (Limnesiidae). The only striking difference between the two taxa is the position of the genital acetabula, which are situated below movable flaps in *Stygomamersopsis* and on such flaps in *Meramecia*.
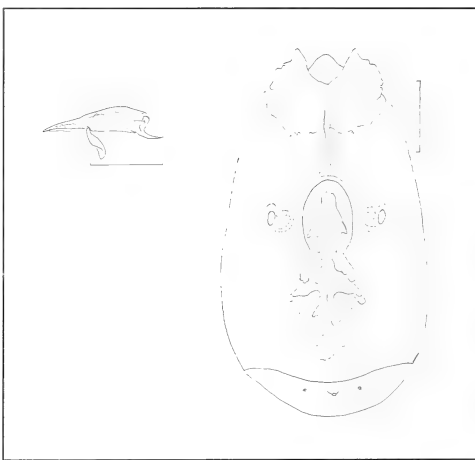
FIG. 112. *Stygomamersopsis anisitsipalpis* Cook, 1974 (male, allotype): Chelicera (left), genital skeleton and outline of body (right). Scale bars = 100 μm. Fig. from paratype, slide 6070, SMF.
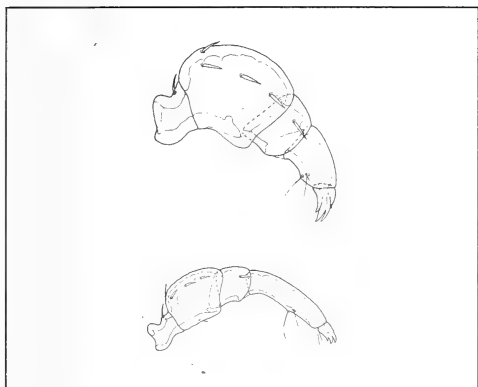
FIG. 113. Palpi of *Stygomamersopsis* Cook, 1974: Palpus of *S. viedmai* (top), Palpus of *S. anisitsipalpis* (bottom). Figs. from Cook (1974).

It has been shown in this study that the position of the genital acetabula is not useful for the separation of families and superfamilies. In the Bharatoniinae, and in some species of the *Nilotonia*-group, tendencies are documented which lead to gradual incorporation of the genital acetabula into the genital flaps. In *Stygomamersopsis* the acetabula are found in the plesiomorph condition (1) clearly below the movable genital flaps and (2) without enlarged basal sclerites. In Bharatoniinae and in the *Nilotonia*-group the acetabula themselves indicate the close relationship between Anisitsiellinae and other Limnesiidae subfamilies. In *Stygomamersopsis* and *Meramecia* adult morphology indicates a close relationship between the two taxa, while the position of the acetabula separates them. It may be justified to shift the genus *Stygomamersopsis* next to the genus *Meramecia* during a revision of the subfamily Neomamersinae. However, as such a revision is beyond the scope of this study, they are kept here as genus "incertae sedis" with the Anisitsiellinae.

Genus: *Psammotorrenticola* Angelier, 1951 [1 spec.]

Typus generis: *Psammotorrenticola gracilis* Angelier 1951. Material examined: *P. gracilis* Nymphal stage; female, "F81, Corse (2B), 2.6.`93 leg. Cit & Ger." CRG. Location of t.g.: Toulouse.

Definition (adults)

Characters of the Anisitsiellinae as defined above and:
- All coxae fused with the ventral shield; anterior region drawn out into a long gnathosomal tube; palps at the anterior end of the camerostome are reduced in size and with most setae reduced.
- Dorsal shields completely covering dorsum, but separated into an anterior and a posterior shield and 5 pairs of platelets which are situated in the dorsal furrow.
- C4 large and with a long medial suture line C4/C4. Insertions of IV-L situated close to the GF in lateral position.
- IV-L stocky; with IV-L-3 and 4 +/– triangular if seen in lateral view; IV-L-6 with claws reduced.

Species included

Psammotorrenticola gracilis Angelier, 1951 was reported with two male and two female specimens from interstitial waters in Corsica (France). The nymphal stage of this species was described by Gerecke (1994).
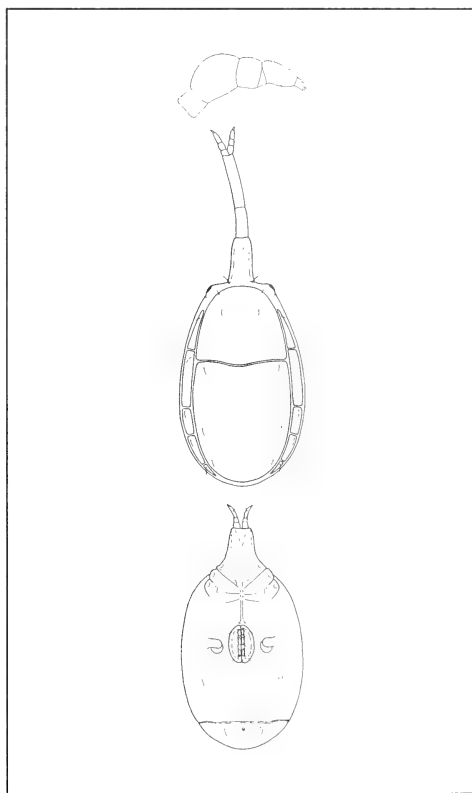
FIG. 114. *Psammotorrenticola gracilis* Angelier, 1951: Palpus (top), dorsal view (middle), ventral view (bottom). Figs. from Cook (1974).

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Inventory (adults)

DS/VS. DS and VS complete. For DS see definition. Excretory pore and flanking glandularia on a separate sclerite.

Eyes. Eye-lenses fused to the ventral shield.

Coxae. See definition above. With protrusible gnathosomal tube.

Cg4. The Cg4 is places in the anteromedial edges of C3.

GF. See definition.

Ac. Three pairs of Ac of equal size, no gap between first, second and third Ac.

I-L-6. With claw tridentate.

IV-L-6. See definition.

Palpus. See definition.

Chelicerae. Together with the long gnathosomal base, the chelicera is elongated and reaches more than 300 µm in total length.

Taxonomic placement

Gerecke (1994) confirms common characters between *Psammotorrenticola* and *Stygomamersopsis* regarding the arrangement of glandularia and setae on dorsal and ventral shields. It seems justified to treat *Psammotorrenticola* as a sister group to *Stygomamersopsis*, with the former differing from the latter in the possession of the protrusible camerostome. The deutonymph of *Psammotorrenticola* shows a distribution of glandularia on the dorsal plates that agrees well with the one described by Smith & Cook (1994) for *Meramecia*. *Psammotorrenticola* therefore provides further arguments for the close relationship between *Psammotorrenticola* and *Stygomamersopsis* on the one hand and between these two and *Meramecia* on the other (as discussed under "*Stygomamersopsis*"). However, for the reasons discussed there, *Psammotorrenticola* is retained as genus "incertae sedis" with the Anisitsiellinae.

Family group of "*Hygrobates*-like and *Mideopsis*-like" Hygrobatoidea

Diagnosis. Diagnostic for the „*Hygrobates*-like and *Mideopsis*-like" Hygrobatoidea is the combination of two characters: (1) the basal ring sclerites of the acetabula are always fused with each other and adjacent sclerites in nymphal stages, (2) movable genital flaps are never present in the adult stage. The sclerites homologous to the genital flaps are either fused to the ventral shield, or fused with the basal sclerites of the acetabula forming one or two ventral plates, or reduced to sclerite rings surrounding the acetabula.

Another feature characterizing the family group to some extent is the absence of the single seta on the ventral surface of the second segment of the palpus. This seta is found in some Hydryphantoidea, in many "*Sperchon*-like" Hygrobatoidea, in nearly all "*Limnesia*-like" Hygrobatoidea, but (with the exception of some species in *Koenikea*) is not found among "*Hygrobates*-like and *Mideopsis*-like" Hygrobatoidea.

Discussion. The group „*Hygrobates*-like and *Mideopsis*-like" Hygrobatoidea includes (1) all 24 families (see Table 11) put under the Arrenuroidea in the system of Cook (1974), and (2) of the Hygrobatoidea (sensu Cook 1974) only the Limnesiidae are excluded and placed with the Torrenticolidae under the "*Limnesia*-like" Hygrobatoidea. Further differentiation would be desirable, as the group is large and exhibits strong differences in adult, nymphal, and larval morphology, as well as in life cycles and behavior. This task could not be included in the present study, which concentrates on the relationship between Limnesiidae and Anisitsiellidae.

If in the keys (Chapter 8) specimens key out as "*Hygrobates*-like and *Mideopsis*-like" Hygrobatoidea, then for further determination the keys of Cook (1974), Gerecke (1994) or Smith & Cook (1991) can be used. None of the families included in the "*Hygrobates*-like and *Mideopsis*-like" Hygrobatoidea has been altered in the present study.

6. SUMMARY

In traditional systematics, the Anisitsiellidae and Limnesiidae were placed in the two superfamilies Lebertoidea and Hygrobatoidea (e.g., Cook 1974).

The investigation of the relationship between Anisitsiellidae and Limnesiidae, presented in this study documents in several cases close relationship between taxa in the two families. The study therefore supports Tuzovski's (1987) view that Lebertoidea and Arrenuroidea should be treated as junior synonyms of the Hygrobatoidea Koch, 1842.

Concept of superfamily Hygrobatoidea

The concept of the superfamily Hygrobatoidea (s.T.) worked out in this study is based on the following arguments:

1. The work of Weigmann (2001) suggests using the concept of segmentation of the water mite body proposed by Grandjean (1934).

2. The concept of Grandjean (1934) comes close to the one used by Tuzovski (1987), and clearly differs from that of Wiles (1997) and others.

3. Although they use different systems, Wiles' results (1997) are congruent with the findings of Tuzovski (1987). Using different names, they denote the presence or absence of homologous setae. Therefore the results of Wiles (1997) confirm Tuzovski's (1987) results on total numbers and on reductions of segmental remnants.

4. Investigations on nymphs and larvae by Tuzovski (1987) show that the results produced by Wiles (1997) and Tuzovski (1987) for adults can be related to the situation in nymphs and larvae; they also show that the same basal chaetom is found in all active life stages.

5. The investigations on segmental remnants show that the common ground plan of the chaetom of the idosoma is found in all Hydrachnellae superfamilies (but not in Stygotrombidiidae) with different reductions of setae in different superfamilies (Tuzovski, 1987).

6. In all life stages, Hydryphantoidea (excluding Wandesiidae), Lebertoidea, Hygrobatoidea and Arrenuroidea (*sensu* Cook 1974) show an idiosomal chaetom with the same reductions. They differ clearly in this character combination from all other superfamilies of the Hydrachnellae (Tuzovski, 1987).

7. The "Lebertoidea - Hygrobatoidea - Arrenuroidea" (superfamilies *sensu* Cook 1974) show synapo-

morphies clearly separating them from the Hydrydphantoidea. (Larvae: (1) reduction of medial eye and propeltidium, (2) fusion of basifemur and telofemur, and (3) adaptation of the larvae to hunt preadult instars of their hosts underwater). The Lebertoidea and Arrenuroidea (*sensu* Cook 1974) are therefore treated by Tuzovski (1987) as junior synonyms of the Hygrobatoidea Koch, 1842.

8. Hydryphantoidea are now separated from the Hygrobatoidea (s.T.) by plesiomorphies only.

9. In this study, the superfamily concept of Tuzovski (1987) is tested for its potential to provide a phylogenetic approach to the group. Therefore a data matrix was formed, based on the data for the idiosomal chaetom given by Tuzovski (1987), as well as on some other (mainly morphological) data from all life stages. The cladogram produced with HENNIG86 (Farris 1988), and with Hydryphantoidea as outgroup, places the superfamilies as (Hydryphantoidea (Hygrobatoidea (Wandesioidea (Hydrachnoidea (Hydrovolzioidea (Piersigioidea (Eylaoidea Limnocharoidea))))))) (Length = 13; Ci = 92; Ri = 87) [Pontarachnoidea not included].

As a result of the above summarized considerations it is suggested to follow Tuzovski (1987) and to treat Lebertoidea and Arrenuroidea (*sensu* Cook 1974) as junior synonyms of the Hygrobatoidea Koch, 1842.

Taxonomic changes in the Hygrobatoidea

Thirty-Five families are included in the Hygrobatoidea (s.T.). The taxonomic investigations in this study refer solely to "anisitsiellid-like" water mites. Therefore, only those taxa are redefined which include or exhibit direct relationships to "anisitsiellid-like" water mites. Several families of the "*Sperchon*-like," and all 24 families of "*Hygrobates*-like and *Mideopsis*-like" Hygrobatoidea (s.T.) are not treated.

Following the ideas of Welbourn (1991), Smith & Cook (1991) and others, larval characters are taken as more conservative than adult characters. Therefore the changes in higher systematics suggested in this study are based on a reassessment of larval characters (see discussions of larvae in chapters "Hygrobatoidea," "Bandakiopsiidae," and "Limnesiidae").

Additionally, the organization type of the provisory genital field of the deutonymphal stage is used as a key character for the systematics of the Hygrobatoidea (s.T.).

Misleading, but of major importance in former systematics, were the adult characters "extent of secondary sclerotization of the idiosoma" and "position of acetabula in the genital field." Approaches based on these characters led to contradictions in the taxonomic system (e.g., placing the two sexes of a single species in two different superfamilies).

The adult characters "organization type of the coxal groups" and "shape of the chelicera" are among the characters investigated which proved to be useful for the alternative redefinition of genera and genera groups.

The taxonomic analysis produced in this study is based on characters of all active life stages and includes solutions for numerous systematic problems. The following synthesis brings together the suggested taxonomic changes. At the same time, it proposes a new scenario as a basis for future discussion and research.

Superfamily Hygrobatoidea Koch, 1842 (s.T.)

The Hygrobatoidea (s.T.) are divided into three familygroups. These family groups are different in larval, deutonymphal and adult characters. They can be distinguished on the basis of differences in the provisory genital field of the deutonymphs and the genital field of the adults.

Family group "*Sperchon*-like" Hygrobatoidea (s.T.)

Members of this group are characterized by the organization type of the provisory genital field with their acetabula not (!) fused to the homologs of the genital flaps in deutonymphs.

The following 6 families are included: Sperchontidae, Rutripalpidae, Bandakiopsiidae fam. nov., Teutoniidae, Oxidae, and Lebertiidae.

The Anisitsiellidae, which were formerly placed next to the families listed here, are split off into several parts. Twenty-six genera are shifted to the family Limnesiidae, and placed there in the subfamily Anisitsiellinae stat. nov. and two new subfamilies. Three genera are placed in the Bandakiopsiidae fam. nov.

Family Bandakiopsiidae fam. nov.

The family Bandakiopsiidae is based on larval and adult characters that indicate a position close to Sperchontidae, Rutripalpidae and Teutoniidae, and clearly separate from the "*Limnesia*-like" Hygrobatoidea.

Additionally the provisory genital field of the deutonymphal stage indicates that it is a member of the "*Sperchon*-like" Hygrobatoidea. Bandakiopsiidae fam. nov. includes the 3 genera *Bandakiopsis, Cookacarus* and *Oregonacarus.*

Genus *Bandakiopsis*

Bandakiopsis phaluti sp. nov. is described from the Himalayas. The new species leads to an amphipacific distribution of the genus and family, which was formerly only known from western North America.

Family group "*Limnesia*-like" Hygrobatoidea (s.T.)

Members of this group are characterized by the combination of two characters: (1) in deutonymphs the acetabula are (!) fused to the homologs of the genital flaps, and (2) movable genital valves are present in female adults (the males of some taxa possess a genital field in which the genital valves are fused to form immovable plates, others possess movable genital valves).

The family group includes the 2 families Torrenticolidae and Limnesiidae.

Family Limnesiidae

Most of the genera which were formerly placed in the Anisitsiellidae are in this study included in the Limnesiidae and placed there in 3 subfamilies. As none of the other subfamilies is altered, only the 3 newly adopted subfamilies are treated in this study.

Subfamily Bandakiinae subfam. nov.

Larvae of Bandakiinae subfam. nov. differ from all other Limnesiidae in the presence of seta sC3, which is reduced in all other known larvae of the Limnesiidae. They share with other "*Limnesia*-like" Hygrobatoidea, and with known larvae of *Hygrobates* and *Atractides*, the reduced size of the anal setae, and differ in this character from the "*Sperchon*-like" Hygrobatoidea.

Deutonymphs differ from Torrenticolidae in the organization type of coxae and dorsal shields.

Adults share with early derivative taxa of the Limnesiidae the possession of claws on leg 4, and with "anisitsiellid-like" members of the Limnesiidae the possession of movable genital flaps in both sexes.

Genus *Bandakia*

The species groups in the genus *Bandakia* are rearranged. Contra Gerecke (1990), the *anisitsipalpis*-group, the *vietsi*-group, and the *longipalpis*-group are retained. The species *B. mexicana* and *B. wendyae* are placed as species incertae sedis, the former for its highly untypical organization type of the coxae, the latter for differences from the genus in the palpi, in the chelicera, and in the shape of the coxae.

Four new species from the Himalayas (*B. curvipalpis*, *B. gangetica*, *B. himachali* and *B. kulluensis*) are described. They all belong to the *anisitsipalpis*-group, which was formerly known only from North America and Japan.

Genus *Utaxatax*

Four new species from the Himalayas, all belonging to the subgenus *Utaxatax* (s.s.), are described (*U. brahmeri*, *U. crassipalpis*, *U. gereckei* and *U. parvati*). The subgenus, formerly known from North America only, shows an amphi-pacific distribution now.

A *Utaxatax* species with a "mamersopsid-like" palp was discovered for the first time. The presence of both basic types of palpi ("anisitsiellid-like" and "mamersopsid-like") is therefore now documented for 3 "anisitsiellid-like" genera (*Bandakia*, *Utaxatax* and *Stygomamersopsis*).

Subfamily Bharatoniinae subfam. nov.

Larvae of Bharatoniinae are unknown. Nymphs and adults show characters relating them to both "anisitsiellid-like" mites and "limnesiid-like" mites. The position of the acetabula in the genital fields of the adults is striking. They extend along the medial margin of movable genital flaps and are adpressed but not fused to them. This position is exactly intermediate between that typical of the former Anisitsiellidae (acetabula below movable flaps) and the one traditionally used to define Limnesiidae (acetabula fused to the genital flaps).

The two monobasic genera, *Bharatonia* and *Shivatonia* gen. nov., are adopted to the new subfamily. While in the former genus the basal sclerites of the anterior two pairs of acetabula are only slightly sclerotized, in the latter they show heavy secondary sclerotization. In *Shivatonia*, the enlarged basal sclerites of the acetabula are fused on each side and form a pair of chitinized sclerite strips, each of them carrying three acetabula and adpressing on each side to the upper medial border of the genital flaps.

Genus *Bharatonia*

The species *Bharatonia vietsi* Cook, 1967, has been discovered for the first time since the original description. The collection site in the south-western Himalayas is about 1500 km north of the locus typicus.

Genus *Shivatonia* gen. nov.

Shivatonia acetabulensis gen. et sp. nov. is described from collections in streams in Darjeeling (India). Apart from the characters given above, the new species is characteristic in the shape of the strong cheliceral claw, which is bent upwards beyond the level of the upper border of the basal segment.

Subfamily Anisitsiellinae stat. nov.

Anisitsiellidae are reduced to the subfamily Anisitsiellinae for the reasons given above. Bader (1980) raised Nilotoniinae to the family level. However, Nilotoniinae (or Nilotoniidae) grade completely into Anisitsiellinae in the extent of secondary sclerotization of the idiosoma [which was the only distinctive character used in traditional systematics (e.g., Cook 1974)]. Furthermore, larvae of species formerly placed under Anisitsiellinae share striking apomorphies with larvae of species formerly placed under the Nilotoniinae. Nilotoniinae (and Nilotoniidae) are therefore treated as junior synonyms of Anisitsiellinae in this study.

Anisitsiellinae include most of the genera and species that were formerly placed in the Anisitsiellidae. Larvae of 3 species [*Anisitsiella costenus*, *Nilotonia (Manotonia) tegulata*, *Nilotonia (Dartiella) longipora*] are known to science. They share as an autapomorphy the character "insertions of seta V1 fused to a common platelet" and they share as a synapomorphy with all other known larvae of the Limnesiidae, except Bandakiinae, the reduction of seta sC3.

In this study, the Anisitsiellinae are divided into 5 genera groups. In addition, 4 genera are placed as "incertae sedis." In 3 of the genera "incertae sedis" clear indications are given that they could be placed in other subfamilies of the Limnesiidae. However, I have kept them with the Anisitsiellinae because either additional knowledge on larval stages, or the revision of the respective subfamilies, or investigations using genetic methods should first substantiate the inclusion of "anisitsiellid-like" species into taxa at present dominated by "limnesiid-like" species.

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In the *Platymamersopsis*- and the *Anisitsiellides*-groups, genera are included for which additional knowledge on larvae or nymphs may mean that they should be shifted to other taxa (e.g., to the Bandakiinae).

Platymamersopsis-group

The *Platymamersopsis*-group includes the genera *Platymamersopsis, Paddelia* gen. nov., and *Gilatonia*.

The genera share the chelicera type with a typical dorsal elevation in the basal segment, the +/– rectangular C4, and the absence of swimming hairs. The IV-L-6 always lacks claws and is typically shortened or flattened.

Genus *Platymamersopsis*

In the subgenus *Platymamersopsis* (s.s.), the characteristic shape of the chelicera and of the IV-L-6 was checked for 9 of the 11 species.

The subgenus *Neomamersella* is shifted from *Mamersella* to *Platymamersopsis* in view of the shape of chelicera, of IV-L-6, and of the (+/- rectangular) C4. Additionally, *Neomamersella* shares with *Platymamersopsis* the unusually long and strong seta lateral on P2.

Genus *Paddelia* gen. nov.

Paddelia eichhorniae gen. et sp. nov. differs from all other „anisitsiellid-like" water mites in its extremely flattened and paddle-like IV-L-6. It shares with the *Platymamersopsis*-like genera the shape of the chelicera and the +/- rectangular C4.

Genus *Gilatonia*

Newly documented in this study for the monobasic genus *Gilatonia* is the shape of the first three pairs of coxae, projecting well over the anterior of the body proper, and the shape of I-L-5,6 and IV-L-5,6. The figure of the IV-L-5,6 in Viets & Böttger (1974) is misleading, as a leg with broken terminal setae was depicted.

Mamersides-group

Four of the 5 genera included in this group, *Hydrobaumia, Mamersides, Mamersopsides* and *Navamamersides*, are characterized by an anterior-pointing hook on the dorsal border of the basal cheliceral segment.

In the fifth genus, *Mamersopsis*, the state of this character is still undescribed. However, with two of the genera (*Hydrobaumia, Mamersopsides*) it shares a characteristic dorsal sclerotization, composed of one or three shields covering a larger central area, which is surrounded by several +/– rectangular platelets.

Genus *Hydrobaumia*

This monobasic genus is known from a single male specimen from India. The holotype is lost, but during the course of this study unpublished figures made by the late L. Halik, were found in the NMB. Hence new information on the shape of the chelicera, and on the shape and chaetotaxy of the legs, is made available in this study.

Mahemamersides-group

The two genera in this group, *Nilgiriopsis* and *Mahemamersides*, have a IV-L-6 with extremely serrate margins and with the cross-section of this segment +/– rectangular.

Genus *Mahemamersides*

Unpublished REM photographs of *Mahemamersides* produced for the late C. Bader were found in the collection of the NHB. Some of them are shown here to give additional information on *Mahemamersides boveyi*.

Anisitsiellides-group

Included in the *Anisitsiellides*-group are the genera *Anisitsiellides, Zelandatonia* and *Sigthoriella*.

Members of this genera group are found only in Australia, New Zealand and South America.

The chelicerae of adults have a rounded elevation at the posterior end of the basal segment. In the genus *Anisitsiellides*, in 10 of the 11 species a chelicera of such a shape is depicted (exception: *A. tabberabbera*).

Zelandatonia shares with the members of the genus *Anisitsiellides* the possession of swimming hairs terminally on IV-L-5, and the genital field placed posterior to the level of the insertions of IV-L. Unfortunately, the chelicera has not been described. With *Anisitsiellides, Sigthoriella* shares the shape of the chelicera. It differs from the two other genera by the absence of swimming hairs on the legs and the presence of well-developed claws on IV-L-6.

Nilotonia-group

The *Nilotonia*-group unites the genus *Nilotonia* with four genera (*Anisitsidartia, Anisitsiella, Mamersella,* and *Rutacarus*) formerly placed in the Anisitsiellinae. *Manotonia* is now ranked as a subgenus in *Nilotonia*.

Since the descriptions of highly seclerotized *Nilotonia* species from Trinidad (Bader 1995), several species in *Mamersella* and *Rutacarus* can no longer be separated from *Nilotonia*. Since only additional information on larvae or biochemical investigations will be able to clarify the appropriate placement of these species, for the time being they have to remain as species "incertae sedis" in the genera to which they were attributed by former authors.

Genus *Anisitsidartia*

In Cook (1966, 1974) a IV-L-6 of *Anisitsidartia* is depicted in which the long terminal seta is broken. A IV-L-6 with an undestroyed seta is depicted in this study.

Genus *Anisitsiella*

Misinterpretation of the German text in the original description led to the false assumption that *Anisitsiella* possesses an extra pair of acetabula. Instead, the text by Daday (1910) refers to openings lateral to the genital flaps, which are found in *Mamersellides* as well. The type of *Anisitsiella aculeata* has been rediscovered in the collection of the NHB. It is in a very poor condition but allows the conclusion that *Mamersellides ventriperforatus* is a junior synonym to *Anisitsiella aculeata*.

Genus *Mamersella*

The subgenus *Neomamersella* is shifted to *Platymamersopsis* (see there).

Mamersella anomala Hopkins, 1967 is conspecific with *Limnesia auspexa* Cook, 1983. As the name *Limnesia anomala* is preoccupied (Koenike 1895), *Limnesia auspexa* Cook, 1983 becomes the valid name. *Mamersella mesoamericana* and *Mamersella ponderi* cannot be distinguished from *Nilotonia* (*Mamersonia*) at the genus level. They are, however, kept as species „incertae sedis" with *Mamersella* until additional information on nymphal or larval stages is available to clarify their appropriate position.

Genus *Rutacarus*

Out of the 5 species known in this genus, *R. stygius* cannot be distinguished from *Nilotonia* (*Mamersonia*) at the genus level. It is kept as species „incertae sedis" with *Rutacarus* as additional information on nymphal or larval stages is needed to confirm its appropriate position.

Genus *Nilotonia*

The 41 species of *Nilotonia* are arranged in 6 subgenera. All subgenera are redefined. The subgenera *Nilotonia* (s.s.), *Mamersonia* and *Manotonia* differ from the remaining subgenera in the organization of the coxae.

Subgenus *Nilotonia* (s.s.)

Contrary to the information in most publications (e.g., Cook 1974) *Nilotonia* (s.s.) *loricata* does possess swimming hairs.

Four species (*N. loricata*, *N. africana*, *N. indica*, *N. cooki* sp. nov.), all characterized by well-developed swimming hairs, are assigned to the subgenus. The subgenus *Tadagatonia* was based on characters all present in *Nilotonia* (s.s.), for example the existence of swimming hairs, and is hence treated as junior synonym to *Nilotonia* (s.s.).

Nilotonia (s.s.) *africana* is not a synonym of *N.* (s.s.) *loricata*, but a valid species. The figures of Daday (1910) show clear differences between the two species in the chaetotaxy of the legs and in the extent of ventral secondary sclerotization.

The adults assigned to the nymphotype of *Nilotonia indica* by Cook (1967) belong to a new species, described as *N. cooki* sp. nov. The collection in India has yielded additional adult and nymphal stages of the new species, as well as adult and nymphal specimens resembling the nymphotype of *N. indica*.

The subgenus is reported from Africa and India only.

Subgenus *Mamersonia*

I follow Cook (1974) in treating *Mamersonia* as a subgenus of *Nilotonia*. The close relationship between *Nilotonia* (s.s.) and *N.* (*M.*) *amazonica* in the shape of the chelicera and in the chaetotaxy of IV-L-6 is documented for the first time. The only reason for keeping the subgenus *Mamersonia* separate from *Nilotonia* (s.s.) is the absence of true swimming hairs in the former.

Five species are included in the subgenus (*N. amazonica*, *N. biscutata*, *N. monoscutata*, *N. similis*, *N. simoni*).

The subgenus is so far known only from Trinidad and the Amazon region.

Subgenus *Manotonia*

As suggested by Gerecke (1992), *Manotonia* is reduced to a subgenus in *Nilotonia* in this study.

Seven species are included in the subgenus, 6 of them reported from Africa and one new species from the Himalayas.

The subgenus is characterized by modifications in the male genital sclerite (known from 2 species only) and by the chaetotaxy of the legs (thin setae typically absent, IV-L-6 typically with only a few small setae). The species included are *N. gracilipalpis, N. musicola, N. shivai* sp. nov., *N. petri, N. scutata, N. tegulata, N. testudinata* and *N. violacea*.

Subgenus *Dartonia*

The subgenus *Dartonia* is characterized by the first coxae, which come close to the GF with their posterior margins, and by the presence of more than one strong setae in terminal or subterminal position.

Four species, all from Asia, are included in the subgenus (*N. caerulea, N. crassipalpis, N. perplexa, N. rizeensis*).

Subgenus *Dartia*

The subgenus *Dartia* shows striking modifications in the genital field indicating a close relationship between *Dartia* and those members of the Limnesiidae in which the acetabula are fused to the genital flaps. In 4 of the 6 species of the subgenus, a sexual dimorphism is found in the terminal segments of the second legs (which are modified in males, while in females they are of usual shape).

The species included are *N. borneri, N. harrisi, N. erzurumiensis, N. vietsi, N. boettgeri* and *N. turcica*.

Four species of the subgenus are reported from Asia, 2 from Europe.

Subgenus *Tadjikodartia*

The monobasic subgenus *Tadjikodartia* is characterized by the coxoglandulare 4 (Cg4) protruding (together with parts of the C3) over C2. As a result, the Cg4 is found in this subgenus just posterior to the suture C1/C2.

Additional material from the Himalayas allows us to synonymize *N. schwoerbeli* with *N. (T.) emarginata*.

The subgenus is now known from Tajikistan, Iran and the Indian Himalayas.

Subgenus *Dartiella*

Fourteen species are included in the subgenus *Dartiella* (*N. catarrhacta, N. fundamentalis, N. gallica, N. hanniae, N. longipora, N. micropora, N. navina, N. ortali, N. parva, N. pontifica, N. pyrenaica, N. rackae, N. robusta* and *N. thermophila*). The subgenus does not show any of the features used to characterize *Dartonia, Tadjikodartia* or *Dartia*. It differs from the other subgenera in the organization of the coxae.

N. buettikeri is a junior synonym of *N. robusta*. The round ventral shield, used by Bader (1980) to characterize *N. buettikeri*, was identified as an egg during investigations on the female holotype.

N. thermophila possesses an elongated terminal seta. Investigations on the holotype have revealed that the insertion of this seta is well visible, although the seta itself is lost in the holotype specimen.

Genera "incertae sedis"

Four genera are placed as genera "incertae sedis" under the Anisitsiellinae. As long as additional information on larvae and nymphs of these taxa, substantiating their appropriate placement, is not available, they are tentatively kept with the Anisitsiellidae.

Genus *Ranautonia*

It is possible that *Ranautonia* is a soft bodied member of the Bandakiopsiidae fam. nov. It shares with this family the hexagonal structure found in several portions of chitinized parts, and the shape and chaetotaxy of the palpi. So far, the genus is only known through a single male specimen described by Viets (1929). Information on the nymphal stage would allow us to decide on its placement.

Genera *Psammotorrenticola* and *Stygomamersopsis*

Stygomamersopsis shares with *Meramecia* (Neomamersinae, Limnesiidae) the chaetotaxy of the palp and the organization form of ventral and dorsal shields. The only striking differences between the two genera is the position of the acetabula (below movable flaps in the former and fused to the flaps in the latter). *Platymamersopsis* is closely related to *Stygomamersopsis*, but has developed a gnathosomal tube.

It may be justified to shift the genera next to *Meramecia* during a revision of the Neomamersinae. Here they are tentatively kept with the Anisitsiellinae.

Genus *Sigthoria*

The males of two genera *Rheolimnesia* and *Siboneya-carus*, both placed in the subfamily Protolimnesiinae, share several characters with *Sigthoria*, such as (1) the organization type of the coxae, especially regarding the shape of C4, (2) the palp with P2 bearing the ventral setae on a short tubercle, and (3) rows of (proliferated) acetabula below the movable genital flaps. The two genera differ from *Sigthoria* in characters such as (1) reduction of the Cg4 and (2) presence of well-developed claws on IV-L-6.

While *Sigtohria* is known from Africa, Asia and Australia, *Rheolimnesia* and *Siboneyacarus* are restricted to Central and South America. Hence, distributional data and adult morphology characters would allow us to interpret *Sigthoria* as a taxon separated geographically at an early stage, but phylogenetically related to *Rheolimnesia* and *Siboneyacarus*. Knowledge on larval stages or further nymphal stages is necessary to decide on the placement of *Sigthoria*. Here it is tentatively kept with the Anisitsiellinae as genus "incertae sedis."

7. FUTURE RESEARCH

Three areas of future research result from the current study:

(1) Which taxa should be selected for a test of superfamily concepts with genetic methods?

The concept of superfamilies suggested by Tuzovski (1987) stands in contradiction to the traditional concepts of Cook (1974), Viets (1987) and others. The present study shows that the investigations on segmental remnants undertaken by Wiles (1997) support the concept of Tuzovski (1987). Because he selected a different set of species for his database is the only reason why Wiles (1997) arrived at different results. A genetic analysis should compare the approaches of Wiles (1997) and Tuzovski (1987). The present study strongly recommends that several taxa omitted by Wiles (1997), but included in the investigation by Tuzovski (1987), should be included in a genetic approach to their phylogeny. The taxa in question are Eylaiidae, Limnocharidae, Piersigiidae, Wandesiidae, and the recently detected Apheviderulicidae (Gerecke *et al.* 1999). This would also allow us to test Tuzovski's (1987) hypothesis that these families are more distantly related to each other than the they are to the 35 families fused into the large superfamily Hygrobatoidea (s.T.).

(2) Testing the new concept for the Anisitsiellidae-Limnesiidae complex during a revision of the "remaining" Limnesiidae

In the present study, three subfamilies have been newly included in the Limnesiidae. They all contain taxa which were formerly placed in the Anisitsiellidae. Four genera are only tentatively kept as genera "incertae sedis" with the Anisitsiellinae (stat. nov. in Limnesiidae). In order to clarify into which subfamily of the Limnesiidae these taxa should be placed, a revision of the remaining subfamilies is necessary.

Such a revision should be based on the results of the present study. This would furthermore also make it possible to examine to what extent the concepts developed here allow a reorganization of the remaining subfamilies.

(3) Testing the new concept for the Anisitsiellidae-Limnesiidae complex with genetic methods

Prior to this study, the inclusion of species of the Anisitsiellidae-Limnesiidae complex in genetic studies on the phylogeny of the group would have led to results which would probably have been irritating as well as difficult to interpret.

The concept presented here and the suggested changes in the systematic system offer clear alternatives which can now be tested with the help of genetic methods.

8. KEYS

Since the following two keys are seen as an extension to the key in Cook (1974), they therefore often refer to figures in that work.

Key 1: Adult key to the Superfamily Hygro-batoidea Koch, 1842 (*sensu* Tuzovski)

1   Acetabula wheel-like, in postgenitale or in the integument . . . . [Pontarachnoidea]
1*   not so 2

2   Acetabula on coxae or in integument . . . . [Hydrovolzioidea, Eylaoidea (*sensu* Tuzovski) in part (= Eylaiidae)]
2*   Acetabula in genital field 3

3   Palp not chelate 4
3*   Palp chelate   [Hydrachnoidea, Hydrodromidae, Hydryphantidae in part]

4   Mouth opening not surrounded by a large circular, membranous fringe 5
4*   Mouth opening surrounded by a large circular, membranous fringe . . . . [Limnocharoidea, Piersigioidea (Note: Adults of Apheviderulicidae Gerrecke *et al.* (1999) are still unknown)]

5   None of the acetabula stalked 6
5*   Some of the acetabula stalked . . . . [Hydryphantoidea in part (= Hydryphantidae in part)]

6   Body soft and greatly elongated; a heavy seta present at dorsodistal end of P4 . . . . [Hydryphantoidea in part (= Hydryphantidae in part)]
6*   not so 7

7   Ventral side of P2 with two or three heavy setae, and dorsum and venter with numerous reticulate platelets which surround the glandularia (figs. 260-66, 270-72 in Cook 1974) . . . . [Hydryphantoidea in part (= Teratothyadidae)]
7*   not so 8

8   P2 with a distal row of numerous setae (about 15-25) and P4 with a ventral row of numerous setae . . . . [Hydryphantoidea in part (= Ctenothyadidae)]
8*   not so 9

9   P2 with two long distolateral setae; dorsal and ventral shields present, numerous setae surrounding, and extending posterior to the camerostome (figs. 288, 290, 293 in Cook 1974) (members of this family known only from thermal springs) . . [Hydryphantoidea in part, Fam. Thermacaridae]
9*   not so 10

10   Numerous acetabula located on movable genital flaps; dorsum (and usually venter) either with closely fitting porous platelets or more widely spaced reticulate platelets; posterior coxal groups much longer than wide (figs. 276, 277, 279 in Cook 1974) . . . . [Hydryphantoidea in part (= Rhynchohydracaridae)]
10*   not so . . . . Hygrobatoidea [*sensu* Tuzovski]

Key 2: Families of "*Sperchon*-like" and "*Limnesia*-like" Hygrobatoidea

Artificial key to adults of Hygrobatoidea (s.T.)

1   Acetabula located very close to each other in two medial rows. (The posterior acetabula sometimes smaller and more roundish, shifted laterally or lying at right-angle to the anterior acetabular.) These acetabula typically covered by movable genital flaps, but occasionally the genital flaps show varying degrees of reduction (Fig. 331 in Cook 1974), or the row of acetabula appears to be adpressed to the medial margin of the flaps (Fig. 45, Fig. 46) 3
1*   Genital field not as described above; if movable genital flaps are present, some or all of the acetabula lie on the flaps 2

2   P2 with a single ventral seta. This seta either sessile or located on a tubercle of variable length; seta typically peg-like but sometimes thin or hair-like; openings for insertions of fourth legs usually without large associated projections which extend laterally or posterolaterally [such projections are found in several species of the genus *Koenikea* (figs. 1086, 1088, 1090, 1092 in Cook 1974). However, if in these species a ventral seta on P2 is present, then the palpus is simple, without projections on P3 and with a hair-like ventral seta on P2 (figs. 1084, 1085, 1089)]; if openings for insertions of fourth legs with associated projections, then either ventral seta on P2 peg-like or P3 with strong ventral projections. . . . . [not so: *Mixolimnesia* 1 sp.] Limnesiidae (in part)

2* not so ... „*Hygrobates*-like and *Mideopsis*-like"
Hygrobatoidea
[see Cook 1974, no further treatment in this study]

3   P5 very broad and spatulate when viewed dorsally
or ventrally . . . . Fam. Rutripalpidae
3* not so 4

4   Fourth coxae partially or completely surrounding
a pair of medially placed glandularia (fig. 329 in
Cook 1974) . . . . Fam. Teutoniidae
4* not so 5

5   All legs inserted far forward on body, actual in-
sertions of fourth legs not visible in ventral or lat-
eral views (figs. 477–505 in Cook 1974); ventral
sides of P2 and P3 without projections . . . . . .
Fam. Oxidae
5* not so 6

6   Dorsal and ventral shields present; dorsal shield
typically consisting of a large plate and two or
four anterior platelets or several peripheral plate-
lets; if only a single dorsal plate is present, an in-
dication that it is the result of fusion of the smal-
ler plates is evident; ventral shield with a Y-sha-
ped suture line extending anteriorly from genital
field to tips of first coxae . Fam. Torrenticolidae
6* not so 7

7   Dorsal and ventral shields absent; a Y-shaped su-
ture line extending anteriorly from genital field
to tips of first coxae; suture line between second
and third coxae present anteriorly and posteriorly
but obliterated in middle; palp of characteristic
shape with long distoventral seta on P2 and five
to seven long setae on medial surface of P3 . . .
Fam. Lebertiidae
7* not so 8

8   More than three acetabula on each side (10 to 30)
. . . . 13
8* Three pairs of acetabula 9

9   Fourth legs with well-developed claws; with three
pairs of acetabula; either located on a median sec-
ondary sclerotization adpressed to the inner mar-
gin of the genital flaps as shown in Fig. 46 or third
pair of acetabula at right-angle to the other two
pairs and as elongated as other pairs (Fig. 45);
lateral eyes on platelets, position of lateral eyes and
arrangement of adjacent platelets and glands as
given in Fig. 48 . . . .
Fam. Limnesiidae in part: Bharatoniinae
9* not so 10

10 Gland (= Cg4) on third coxae medial in position;
a suture line on each side extending across the
third coxae immediately lateral to the gland . . .
Fam. Limnesiidae in part: Bandakiinae
10* not so 11

11 Fourth legs with well-developed claws; ventral
and dorsal shield complete; lateral eyes on plate-
lets; P2 without ventral projections but either
with short and blunt seta in ventrolateral posi-
tion or with moderately strong seta in ventrodistal
position; claws at PV well developed Fam. Ban-
dakiopsidae
11* not so 12

12 Fourth legs with well-developed claws; never with
complete ventral shield; lateral eyes typically in
capsules . . . . Fam. Sperchontidae
12* Fourth legs without well-developed claws; how-
ever in one species claws on fourth leg present
(but in this species eyes are not in capsules and
a well-developed ventral shield is present) . . . .
Fam. Limnesiidae in part: Anisitsiellinae

13 Fourth legs without well-developed claws, swim-
ming hairs present . . . .
Fam. Limnesiidae (in part): Anisitsiellinae (i.p.):
Sigthoria
13* not so . . . . Fam. Limnesiidae (in part):
Protolimnesiinae (in part)

9. REFERENCES

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